Floristic response to landscape context in vascular plant communities in *Eucalyptus obliqua* and *Eucalyptus regnans* wet forest, southern Tasmania

by

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Declaration of originality

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Statement of Ethical Conduct

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

Jayne Balmer

24/01/2016

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Part A

Abstract

Theories developed within the paradigm of landscape ecology propose that biodiversity within any given patch will be influenced by the surrounding landscape context (LC). Here LC is defined as the vegetation or land covers surrounding the site. This thesis used empirical vascular plant abundance data from the Huon forest district in southern Tasmania to test the hypothesis that LC influences the floristic composition and successional trajectory of patches within *Eucalyptus obliqua* and *E. regnans* wet forest. Secondary objectives included measuring the spatial and temporal variation in LC of the study area and its association with timber harvesting; describing differences in the response to LC between species and plant groups; comparing the effect size of plant responses to LC with other environmental predictors; finding the spatial and temporal scale at which plants respond most strongly to LC; and determining whether the effect of LC varied in response to disturbance regime differences.

Most studies in landscape ecology have explored the effects of fragmentation on native vegetation in an agricultural matrix. In contrast, forest patches sampled in this study comprised native forest of various ages and successional stages within *intact* to *variegated* landscapes (*sensu* McIntyre and Hobbs 1999[1]) in a frontier region dedicated substantially to timber production. Variation in LC was investigated for the study region using a new metric: the Landscape Context Index (LCI). This metric provided a relative scale of vegetation maturity in areas surrounding any given 50 x 50 m pixel, measured in 500 m, 1 km and 2 km radii. LCI was mapped for three years (1947, 1985 and 2009). The average LCI score was lower in 1985 than 1947, and was lower again in 2009. The greatest declines in LCI score were associated with timber harvesting, although in settled areas conversion to plantations was also an important contributor to LC score decline. The extreme reductions in LCI score observed in the

[1] McIntyre S, Hobbs R (1999) A framework for conceptualising human effects on landscape and its relevance to management and research models. Conservation Biology 13:1282-1292.

period between 1947 and 1985 were not observed in the second period, possibly due in part to the mitigating effect of the Forest Practices Code, which resulted in changes to timber harvesting practices, including increased dispersal and reduced size of clear-felled patches.

Distance to the nearest mature forest edge (DMFE), was used as a surrogate for mature forest influence, a component of LC. Between 15 to 200 m DMFE, there was an observed gradient in assemblage variation, species richness and diversity in all three age classes of silvicultural regrowth forest studied (4–9, 22–28, and 41–45 years since regeneration). These trends were mainly driven by declines in richness and cover of mature forest affiliated species. Factors considered likely to contribute to differences in plant species response to LC are their sensitivity to micro-climatic variation (influenced by proximity to mature forest, and topography) and macro-climatic variation, their capacity to persist through disturbance, and their dispersal mode.

Individual species abundance models for both mature forest affiliated species and pioneer species were stronger (e.g. 38 out of 56 common species using beta regression modelling) when they included both LC metrics and site environmental variables. Although LC was important in explaining variance in species abundance, it typically contributed less to model strength than other environmental predictors, such as soil, climate, topography and disturbance history. Abundance of most pioneer species was associated negatively with mature forest metrics, while the abundance of mature forest affiliated species was associated positively with these metrics. There was little evidence that plant species with bird or wind dispersed seed or that had seed able to persist through disturbance in the soil or in woody capsules were any less associated with LC metrics than species sensitive to disturbance with shorter dispersal capacity. It is therefore possible that such species were responding indirectly to LC through inter species competition, or because they were dependent on animal species sensitive to LC for their pollination or dispersal. LC effects on site micro-climate, soil and browsing pressure, which all vary with distance from edges of mature forest could also be influencing the distribution of species in ways that are associated with the distance from and proportion of mature forest in the landscape. Auto-correlation

between LC metrics and site history are other factors that may be contributing to the observed responses of all plant species to LC metrics.

There was only equivocal support for the hypothesis that floristic responses within regrowth forests are more strongly associated with the LC of the patch at the time that they were last disturbed rather than current LC. Interpretation of the response of vegetation to both the spatial and temporal scale of LC was hampered by the strong autocorrelation in LC scores between scales, and by the sampling methods chosen. The balance of evidence suggests that the LC in the years following disturbance and prior to canopy closure strongly influence the trajectory rate of succession, however colonization and extinction within sites may occur infrequently at any time so that later successional stages are still likely to be influenced by LC at all times.

An interactive effect between proximity to mature forest and fire frequency was observed within secondary regrowth forests, such that patches burnt twice or more since 1898 exhibited greater assemblage differences with distance from the boundary compared with forest burnt only once. This was evidence that the response to LC is partly dependent on disturbance regimes at the site and that succession towards mature forest occurs more slowly in frequently disturbed patches. There was also a poor representation of the dominant rainforest trees and epiphytic ferns in regrowth forest that has colonized abandoned pastures (old fields), irrespective of the LC. Barriers to the colonization by rainforest tree species within old field regrowth may include the maintenance of more open canopy structure for longer periods than typical in uncleared regrowth forest disturbed by single fire events.

An examination of all results in conjunction with those of other empirical studies suggest that successional trajectories in the species composition of wet eucalypt forests may be altered by changes in landscape configurations in response to silvicultural practices and changes in climate and associated fire regimes. Given the association between LC and succession in forest patches, the observed reductions in mean LCI scores across the study region may signal that recovery from the effects of wildfire, extreme climate events, and harvesting may be slower at the site level. If so, then current LC patterns reflect a reduction in resilience at the landscape scale. Predicted changes in climate and associated fire regimes may make local extinctions

more likely in areas of low LCI score. In the context of landscape planning, although dispersal and pollination distances for most vascular plants is best measured in tens of metres rather than kilometres, landscape planning at 500 m to one kilometre may be sufficient to avoid local extinctions at finer scales and thereby prevent range contractions. Silvicultural methods and land management practices that may avert future losses in landscape resilience are discussed.

Aim of thesis

The primary aim of this thesis was to test the hypothesis posed by connectivity theory that landscape context (LC) influences the biodiversity of the patch. This hypothesis was tested for Australian wet eucalypt forest within a 79,000 ha region within the Huon district forests, Southern Tasmania (-43^{o}10'0", 146^{o}55'0", Figure 2–1). This region has been fragmented by stochastic disturbance events including wildfire and timber harvesting, and to a much lesser extent by conversion of forest to agricultural land and timber plantations. The thesis investigated the relative importance of LC compared with immediate site environment for the abundance of individual species and species groups and whether successional processes were influenced by LC. The results of these investigations were used to review currently accepted theory of succession for Australian wet eucalypt forest and assess to what extent disturbance regime change may affect biodiversity conservation at the site, local landscape and regional scale.

Subsidiary objectives were to identify the species and species groups most sensitive to changes in disturbance regimes and landscape fragmentation as well as to assess landscape-metrics and parameters that may be useful for landscape planning and management.

Overview of thesis structure

The thesis abstract, aims, structure, acknowledgements and table of contents are all located in the preliminary sections of Volume A of this thesis.

Chapter one provides a general overview of the literature and identifies the knowledge gaps which formed the foundation to the research work undertaken for the thesis. Chapters 2 to 6 are presented as stand-alone studies, each with an abstract, introduction, methods, results and discussion section. Chapter 7 summarises how each of the earlier studies contributes to satisfying the overall thesis aims in the context of other empirical studies of wet eucalypt forest and successional theory.

Appendices containing supplementary material for every chapter are provided in the second volume of this thesis, Part B. The references from each of the chapters in Part A are collated at the end of this volume. References cited in the Appendices are collated at the end of Part B.

Chapter 1: Aim and introduction

The overall aim of the thesis and the thesis structure is followed in Chapter 1 by a general introduction to the contribution of forest clearance and fragmentation to global biodiversity loss, and the regional concern that timber harvesting may be impacting on biodiversity at the regional scale also. The wet eucalypt forest is described and important terms defined within a general review of wet forest dynamics. A review of some aspects of the landscape ecology literature is provided together with definitions of terms used within the thesis. In particular the potential responses of plant species to their landscape are proposed. The important gaps remaining in the literature from which the initial thesis aims were developed are identified at the end of the chapter.

Chapter 2: Landscape context variation, 1947 to 2009

Chapter 2 provides an overview of the environment and land uses within the study region and documents the changes in the distribution and demography of forests from

1947 to 1985 and 1985 to 2009. A new metric, the LC index (LCI), is described and used for measuring LC in the study region over the two time periods. This study investigates:

- how LC varies spatially and temporally in the study area;
- how LC variation is affected by the precision and scale of the data;
- to what extent timber harvesting has resulted in LC change compared with other disturbance types; and
- whether adverse LC change caused by timber harvesting has been mitigated by changes in industrial practice, policy and regulation.

Chapter 3: Floristic response in silvicultural forest to distance from the mature forest edge

This chapter investigates three age classes of clear-felled forest (also known as clear-cut) and tests the hypothesis that distance from the mature forest edge (DMFE) is associated with floristic variation in regrowth wet eucalypt forest. After establishing that such an association was present, the study goes on to address the related questions:

- Is the floristic association with DMFE driven by both pioneer and rainforest species?
- Does the strength of association with DMFE vary among different plant persistence and dispersal types?
- What is the response magnitude of the floristic association with DMFE and does the magnitude vary in response to other environmental predictors and the importance of rainforest species in the adjacent mature forest?
- What is the estimated depth of mature forest influence (DFI) for species assemblage?

Chapter 4: Species response to landscape context

In this chapter the species characterising successional stages of the wet forest sere were determined. The relative importance of LC and immediate site environment was estimated at the level of floristic assemblage and individual species in forests of different ages. The importance of LC was estimated using several different vegetation metrics, each calculated at several temporal and/or spatial scales. These metrics, including patch size metrics, the proportion of mature forest in the surrounding landscape and proximity to nearest mature forest (PM), were evaluated to determine which had the strongest association with floristic variation. The relationship between species traits and response to LC metrics was also investigated.

Chapter 5: Temporal scale of response to landscape context

This chapter tested the hypothesis that LC will have its greatest influence on the successional trajectory of wet eucalypt forest at and immediately following disturbance. Two metrics (LCI and PM) were used to test at what temporal scale LC was associated strongly with floristic responses in wet eucalypt forests. Assemblages within different forest age classes were examined together with the richness and cover of mature forest indicator (MFI) species, total species richness, epiphytic fern richness and woody pioneer species richness – within silvicultural regrowth forests. The total MFI species richness and MFI species richness in mature forest was examined also.

Chapter 6: Landscape influence on forest establishment in old fields

This chapter investigated regrowth wet eucalypt forest located in old fields within a small region of Tasmania's Southern Forest and compares their floristic composition with similar aged forests in areas that had never converted and to mature forest. In particular it set out to answer the following questions:

- Does the composition of regrowth in old fields differ from other sites?
- Is the floristic response to LC the same for regrowth in old fields as other sites?

- Is the similarity to mature forest and the response to LC of this response the same for regrowth in old fields as other sites?

Chapter 7: Final discussion

In this final chapter the successional processes in wet forest are re-examined in the light of the results of this study and other available empirical data for wet eucalypt forests. A revision of Ashton's (1981b) model is provided specifically for Tasmania's southern forests. The implications of the results for forest management are discussed in the context of previous advice provided by other workers (e.g. Lindenmayer et al. 2006; Groeneveld et al. 2009; Krauss et al. 2010). A brief review of the strength and weaknesses of the approaches taken in this study are provided together with some of the key unanswered questions requiring further research.

Chapter 8: References

All references cited within Part A of this thesis are collated in chapter 8. Additional references cited within Part B are provided as a separate list in Appendix 8.

Glossary of some terms and abbreviations

DMFE	Distance from mature forest edge.
fragmentation	The process of subdivision of habitat and associated reduction in size and amount of habitat and increased isolation from other habitat patches.
habitat subdivision	Lindenmayer and Fischer (2006) define it as "the subdivision of a single large area of habitat into several smaller areas."
habitat	Lindenmayer and Fischer (2006) define it as "the environment suitable for a particular species."
landscape context	The vegetation or land covers surrounding the site
LC	see landscape context
LC heterogeneity	The variability of habitats /land uses etc, within the surrounding landscape; presence of a greater range of structural diversity.
LCI	Metric score using the Landscape Context Index, a scoring system that calculates the weighted average of stability scores for vegetation classes within the surrounding landscape defined by a particular radius and year. See Chapter 2.
matrix	Lindenmayer and Fischer (2006) define it in terms of Forman (1995) landscape mosaic model as the dominant and most extensive land cover in the landscape surrounding a habitat patch.
mature forest	In the context of Tasmanian wet eucalypt forest this is used to include all forest with mature trees more than 110 years in age. In the context of other studies it is likely to refer to forests mature trees

	and at least some structural and floristic characteristics of late-stage forest communities.
mature forest influence	A process which leads to an effect on biodiversity that is related to the presence of mature forest in the surrounding landscape.
mixed forest	Defined for Tasmania by Gilbert (1959) as forest with a eucalypt canopy over an understorey dominated by rainforest species (see definition of rainforest).
older regrowth forest	Wet eucalypt forest in which eucalypts derived from disturbance by either timber harvesting or wildfire between 50 and 110 years previously were present. Mature trees were also likely to have been present in such forests, allowing them to also be classified as mature forest.
oldgrowth forest	In the context of Tasmanian wet eucalypt forest this term is applied to forest without a known history of disturbance by timber harvesting or wildfire in the past 110 years.
patch	Lindenmayer and Fischer (2006) define it in terms of Forman (1995) landscape mosaic model as "relatively homogenous nonlinear areas that differ from their surroundings." In the context of the studies undertaken for the research patches were homogenous areas defined according to the year they were last disturbed by a timber harvesting event (coupe) or wildfire or in some cases by their coverage by a particular vegetation class defined in terms of age and structure.
rainforest	Rainforest in Tasmania is defined by Jarman and Brown (1983) "as forest vegetation (trees greater

	than 8 m) dominated by species of *Nothofagus, Eucryphia, Atherosperma, Athrotaxis, Lagarostrobos, Phyllocladus* or *Diselma*." Note this definition applies to the for the cool temperate areas in Tasmania with rainfall above 1000 mm.
regrowth forest	Also regrowth, or regrowth forest, is any wet eucalypt forest in which eucalypts regenerating from disturbance in the previous 110 years have established. Mature eucalypt trees may have survived the last disturbance leading to the presence of a multi-cohort stand.
secondary forest	Any forest which has regenerated following catastrophic disturbance such as clearance, timber harvesting or wildfire and has not developed an assemblage characteristic of late-stage/oldgrowth forest communities.
silvicultural regrowth forest	Regrowth forest derived from timber harvesting, in the context of the research work undertaken for this thesis silvicultural forests in the current landscape were derived from harvesting operations since 1959. Regrowth forests older than 50 years of age derived from selective harvesting operations prior to 1959 were classified as older regrowth forest in current landscapes.
wet eucalypt forest	Kirkpatrick et al. (1988) define wet eucalypt forest as forests dominated by *Eucalyptus* species over an understorey "dominated, either singly or in a mixture, by rainforest trees, broad-leaved shrubs, or ferns (from which [they] exclude bracken and resurrection plants such as *Cheilanthes*)".

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Plates

Plate 1a. Rainforest understorey in mature eucalypt forest (photograph by Grant Dixon)
Plate 1b. Boundary between mature eucalypt forest and clear-felled coupe (photograph by Sue Baker)
Plate 1c. Silvicultural regrowth, c. seven years old (photograph by Tom Baker)
Plate 1d. View of thesis study area, the Experimental Forest Landscape (EFL), westward view towards the Tasmanian Wilderness World Heritage Area (photograph by Perpetua Turner)

Plate 2. Regeneration in recently harvested clear-fell sites. **Plate 2a.** Six months after clear-felling, this site is dominated by the Asteraceous forb, *Senecio linearifolius,* and seedlings of the broad-leaved tree *Pomaderris apetala* (the understorey dominant prior to harvest, apparent in the adjacent forest visible in the background of the photo). **Plate 2b.** Some tree ferns (*Dicksonia antarctica*) survive the mechanical disturbance of clear-felling and are able to resprout after the high-intensity regeneration burn. In this image the herbs and soft leaved pioneer ferns are the dominant ground covers, less than six months since regeneration. **Plate 2c.** This c. five year old site shows dense recovery of eucalypt saplings. The aerially-sown eucalypt seed germinates well on the mineral soil exposed by the high-intensity regeneration burn.

Plate 3. A 44 year old silvicultural regrowth site regenerated in 1966, which is dominated by *Eucalyptus obliqua* over an understorey of *Pomaderris apetala*. Leaf litter dominates the ground layer. The size of the previous cohort of eucalypts is indicated by the stump in the lower image.

Plates 4a & b. Thirty five year old silvicultural regrowth (regenerated in 1975), dominated by *Eucalyptus obliqua* over an understorey of *Nematolepis squamea* and *Monotoca glauca* (Epacridaceae), with a ground cover of tall tussock sedge *Gahnia grandis* and bracken fern, *Pteridium esculentum*. **Plate 4c.** Even in silvicultural regrowth mature trees, left standing as seed trees in the harvest site or in adjacent mature patches, cause disturbance when they fall and create tree fall gaps and a large accumulation of debris. **Plate 4d.** *Eucalyptus obliqua* stump in silvicultural regrowth forest surrounded by *Gahnia grandis*. Understoreys of *Monotoca glauca* and *Gahnia grandis* are typical of more acid soils and poorly drained sites.

Plate 5. Mature forest dominated by *Eucalyptus regnans,* last burnt in a wildfire early in the twentieth century (~1906). **Plate 5a.** *Pomaderris apetala* is still common, fallen trees (wind thrown?) established new vertical leaders. **Plates 5b & 5c.** Shade-tolerant and slower growing broad-leaved Asteraceous tree *Olearia argophylla* is the dominant understorey species and the wind-dispersed rainforest tree *Atherosperma moschatum* is also common (branch in the foreground at the bottom right of plate 5c).

Plate 6. Mixed forest burnt in the 1934 wildfires, in which old growth trees of *Eucalyptus regnans* are still present. **6a.** Logs are often moss covered and as they decompose become a nursery for rainforest seedlings and ferns. **6b.** In mature forest on fertile sites, such as this, there is often a high diversity of ferns, including epiphytic ferns such as *Rumohra adiantiformis* and *Hymenophyllum flabellatum,* growing on logs and tree trunks especially the tree fern trunks, *Dicksonia antarctica*. **6c.** An insect trap set to catch winged beetles is located in the bottom right of the picture; the ground fern, *Polystichum proliferum*, and mid-layer of tree fern, *Dicksonia antarctica*, are common in the understorey of forests on relatively fertile soils.

Plate 7. Fern ground covers sometimes present in wet eucalypt forest. **7a.** A site with 28 year old silvicultural regrowth regenerated in 1983 still retains a dense ground cover of the pioneer ferns *Hypolepis rugosula* and *Histiopteris incisa,* especially near the mature forest edge. Small rainforest trees of *Nothofagus cunninghamii* and tree ferns that resprouted following the regeneration burn are scattered through this site. **7b.** This 43 year old silvicultural regrowth, regenerated in 1966, still has a ground layer dominated by *Pteridium esculentum* beneath a mid layer of *Acacia dealbata* and a canopy of *Eucalyptus obliqua.* A frequent history of fires, and poor soils have left this site depauperate in rainforest and other species. **7c.** This mature forest has a ground layer patchily dominated by the fern *Blechnum wattsii*. This species is more characteristic of thamnic rainforest understoreys associated with relatively acid soils, along with a richer diversity of rainforest trees, including *Eucryphia lucida* and *Anodopetalum biglandulosum*. It is sometimes prolific in canopy gaps created by the death of *N. cunninghamii* killed by myrtle wilt.

Plate 8. Mixed forests with a dense tangle of shrubs and small trees in the understorey are typical of relatively acid soils. **Plate 8a.** Upper canopy of *Nothofagus cunninghamii*. **Plate 8b.** *Anodopetalum biglandulosum* and other trees. **Plate 8c.** Saplings of *Nothofagus cunninghamii* and other rainforest trees surrounding buttress of a fire-scarred old growth tree of *Eucalyptus obliqua.* The broad-leaved shrub *Anopterus glandulosus* is in the bottom right of the plate.

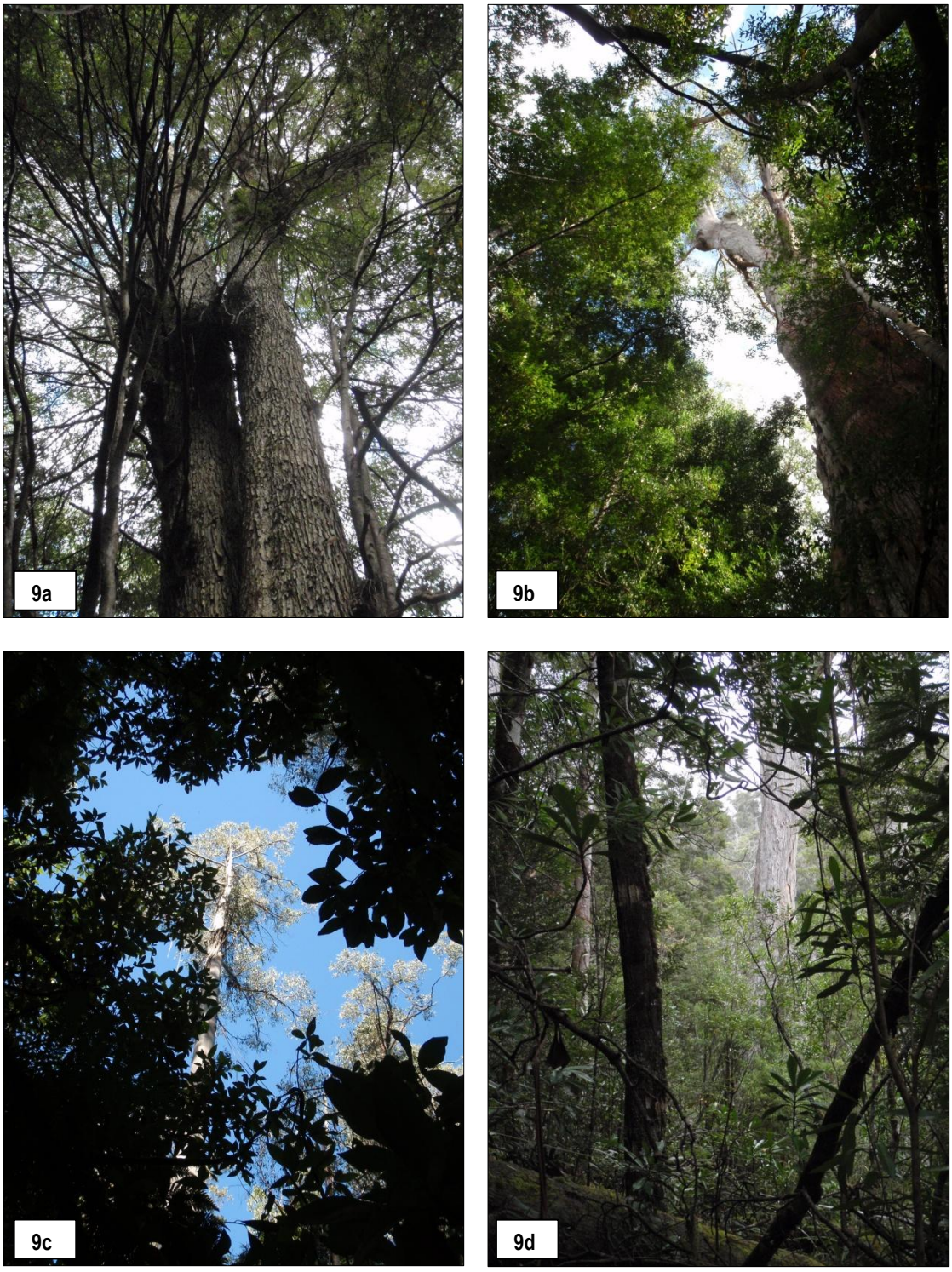

Plate 9a. The two large *Acacia melanoxylon, this species usually forms a sparse emergent canopy above the main understorey dominant and below the taller eucalypt canopy*. Plate **9b**, **9c** & **9d**. Wet eucalypt forests dominated by *Eucalyptus regnans.*

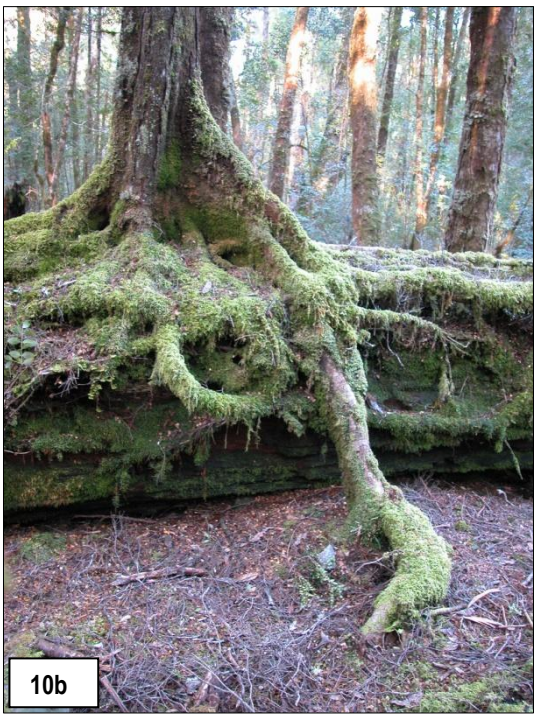

Plate 10. Mixed forest understoreys. **Plate 10a.** Mature rainforest trees, including *Nothofagus cunninghamii* and *Atherosperma moschatum*, over sparesly scattered tree ferns, *Dicksonia antarctica*. Note the moss covers branchwood on the ground and lower tree trunks and there is a litter layer of *N. cunninghamii* branchlets (Photograph by Grant Dixon). **Plate 10b.** Mature tree of *Nothofagus cunninghammii* that germinated and grew on a eucalypt log (Photograph by Greg Jordan).

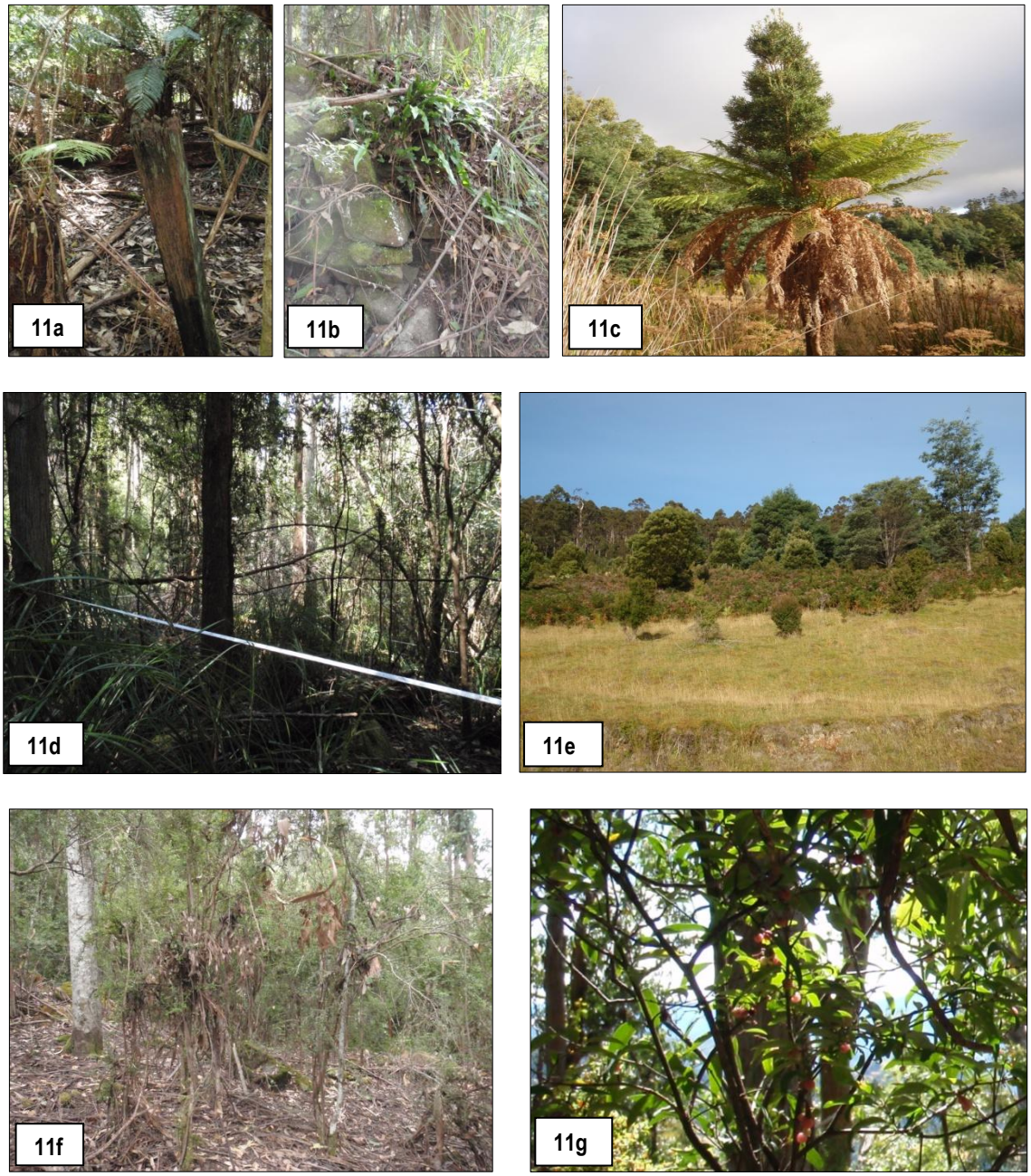

Plate 11. Old field areas. **11a.** Relict fence post dividing two old fields. **11b.** Cairn of stones cleared from old field area. **11c**. Recently abandoned field showing a tree fern, *Dicksonia anarctica* with a sapling of the tree *Pittosporum bicolor* (Pittosporaceae) growing from the crown.The graminoid, *Juncus* sp. and various forbs have invaded around the base of the tree fern. **11d.** Regrowth forest on area of old field. **11e.** A field being colonized by ground fern, *Pteridium esculentum* and the tree *Acacia dealbata.* **11f.** *Coprosma quadrifida* (Rubiaceae) is the predominant understorey cover in this regrowth forest in an old field. **11g.** Fleshy fruits on the tree *Tasmannia lanceolata* (Winteraceae), within the regrowth forest understorey in an old field.

Plate 12. Satellite imagery obtained from Google Earth, demonstrating the distribution of recent timber harvesting operations in the same part of the study area (Huon, Picton and Arve River Valleys) taken three years apart: March 2010 (above) and September 2013 (below).

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"Together they went down into the forest .... There they stood still, they were struck dumb; they stood still and gazed at the forest. They saw the height of the cedar, ... The hugeness of the cedar rose in front of the mountain, its shade was beautiful, full of comfort; mountain and glade were green with brushwood."

The epic of Gilgamesh, 2006 edition, translation by N.K. Sandars first published in 1960, Penguin Books, London, pp. 16–17. [From an epic poem dating from the third millennium BC, compiled on clay tablets circa 1200 BC]

Chapter 1 Introduction

1.1 Abstract

Land clearance, associated habitat fragmentation, reduced landscape heterogeneity and changes in disturbance regimes are known to be contributing to global biodiversity losses . The extent to which timber harvesting practices may be contributing to loss in floristic diversity within wet eucalypt forest at a regional scale in Tasmania has not previously been investigated using a landscape ecology approach. This chapter reviews both the literature relating to landscape ecology and the ecology and successional dynamics of wet eucalypt forest. The existing landscape ecology literature has demonstrated that the responses of individual species and communities to habitat loss and fragmentation vary greatly depending on spatial and temporal scale, species traits and ecosystem dynamics. The great variation in responses and the relative paucity of vascular plant studies undertaken within native forest landscapes demonstrate a need to undertake research to determine the importance of landscape ecology for plants within wet eucalypt forest. Potential responses of wet eucalypt forest plant species to their landscapes are hypothesized.

1.2 Introduction

The two most widespread and commercially important lowland wet eucalypt forest communities in Tasmania are dominated by *Eucalyptus obliqua*[2] and *E. regnans* (Harris and Kitchener 2005). The overall aim of this research thesis is to determine the importance of surrounding landscapes on the distribution and abundance of individual plant species, floristic diversity, and floristic assemblages compared with the environmental and historical factors already known to impact on these forest types (Kirkpatrick et al. 1988; Hickey 1994; Corbett and Balmer 2001; Doran et al. 2003; Turner et al. 2009). This thesis investigates whether changes in landscape fragmentation and disturbance caused by timber harvesting and wildfires are impacting on vascular plant diversity independent of underlying environmental

[2] Taxonomic nomenclature for all Tasmanian plant names mentioned in this thesis follows de Salas and Baker (2014) unless otherwise stated.

variation. By expanding knowledge of the importance of landscape scale processes, improvements may be made to models of successional dynamics, and to tools and guidelines for landscape management and planning.

Global species' extinction rates are estimated to be at between 1000 and 10,000 times higher than the background rate (Singh 2002). Deforestation and associated landscape fragmentation has been described as the major cause of the current global biodiversity crisis (Glanznig 1995; Myers 1996; Brooks et al. 2002; Laurance 2007; Boakes et al. 2010) although Wright and Mueller-Landau (2006) argue that deforestation will slow in response to demographic factors. Indeed the global rate of forest loss did reduce in the decade to 2005 (FAO 2005). The slowing in losses is in part due to the globally increasing rate of both passive and active reforestation of cleared land (Chazdon 2008; Cramer et al. 2008). Therefore, it is likely that there remains a net replacement of mature forest with younger forest.

Recent research suggests that human-induced climate change could pose an even greater threat to biodiversity conservation than deforestation and fragmentation, compounding the problem (Malcolm et al. 2006). Fire regimes, logging disturbance and fragmentation have also been argued to have caused biodiversity loss (Saunders et al. 1991; Williams et al. 2001; Australian Bureau of Statistics 2002; Kingsford et al. 2009).

In the 1990s, Australia had the fifth highest rate of land clearance in the world (Australian Bureau of Statistics 2002; State of the Environment Committee Australia 2002). In 2006 Australian Bureau of Statistics reported that 20% of forest and woodland had been cleared or modified in Australia since 1788, while a recent estimate for Australia's forest loss is now 40% (Bradshaw 2012). Although the rate of clearance in Australia has substantially declined in the last decade, the remaining forest is highly fragmented and degraded, and the degradation continues (Bradshaw 2012).

There has been ongoing conflict over forest management in Tasmania (Kirkpatrick 1981; Helsham et al. 1988; Young 1991; Buckman 2008). Although 45% of Tasmania's remaining forests are now contained within a comprehensive, adequate

and representative reserve system, it is likely that regional population viability of many taxa remains dependent on unreserved land (Lindenmayer et al. 2006; Lindenmayer et al. 2008a). In the decade following 1996 when the Tasmanian Regional Forest Agreement became law, 5.9% of wet eucalypt forests were replaced by plantations or non-forest (Tasmanian and Australian Governments 2007). In 2007 Australian Green Senator, Dr Bob Brown, took Forestry Tasmania to the High Court of Australia. He contested that logging posed a threat to species listed under the *Environmental Protection and Biodiversity Conservation Act 1999*. This case was supported in the initial hearing. Forestry Tasmania ultimately won the case on appeal, after the law was changed (Allchin et al. 2013). The case highlighted that the viability of some populations remain uncertain given ongoing changes to the landscape by logging. This research project forms part of a multi-disciplinary project initiated by Forestry Tasmania to investigate the impact of landscape change and fragmentation on biodiversity.

1.3 Wet eucalypt forest and their dynamics

Temperate wet (humid) forests of Australia are floristically and climatically distinct from those of the northern hemisphere (Ovington 1983). These forests were once widespread across Gondwana. Due to the aridification of the Australian continent this biome has contracted to refugia, concentrated in southeastern Australia (White 1986). The low nutrient status of Australia's soils resulted in the evolution of a scleromorphic flora that was advantaged further by increasing aridity (Loveless 1961, 1962). Increasing fire frequencies associated with drier climates and the arrival of people also contributed to the expansion and radiation of this flora, especially the genus *Eucalyptus sensu lato* (Jackson 1999a). It is the mix of sclerophyllous and orthophyllous plants that distinguish Australia's temperate wet forests from forests elsewhere in the Southern Hemisphere and may make them sensitive to changes in disturbance and climatic regimes (Ovington and Pryor 1983; Mackey et al. 2002; Balmer et al. 2004; Byrne et al. 2011).

Kirkpatrick et al. (1988) define wet eucalypt forest as forests dominated by *Eucalyptus* species over an understorey "dominated, either singly or in a mixture, by rainforest trees (*sensu* Jarman and Brown 1983), broad-leaved shrubs, or ferns (from

which [they] exclude bracken and resurrection plants such as *Cheilanthes*)". Incorporated within this definition are the mixed forests (*sensu* Gilbert 1959), which comprise eucalypt forest with an understorey of rainforest vegetation.

The most widely accepted definition of rainforest in Tasmania is that of Jarman and Brown (1983) who defined it "as forest vegetation (trees greater than 8 m) dominated by species of *Nothofagus, Eucryphia, Atherosperma, Athrotaxis, Lagarostrobos, Phyllocladus* or *Diselma*." They qualified their description by embracing within their definition, vegetation dominated by species such as *Anodopetalum,* which are usually understorey species but occasionally achieve greater importance. However, their definition limited rainforest to communities occurring in cool moist environments that were dominated by plant members of the relict sub-element of Gondwanic flora. Thus it excluded the possibility of classifying vegetation dominated by *Eucalyptus* species as rainforest.

The wet eucalypt forests represent part of the same ecological sere as cool temperate rainforest, occurring in a mosaic with rainforest, scrub and non-forest communities within regions where rainfall exceeds 1000 mm per annum and 50 mm monthly rainfall (Ashton 1981c; Jackson 1999b). The wet eucalypt forests are associated with fire intervals of between 25 to 350 years (Jackson 1968; Wood et al. 2010). Fire in this forest kills many individual plants, clears much of the above ground biomass, exposes mineral soil, creates a nutrient rich ash-bed, while the associated smoke and heat trigger the germination of many light-demanding species (Ashton 1981b; Bell 1999). Vegetative resprouting and seedling regeneration rapidly follow fire, and canopy closure is usually complete within the first two to three decades (Ashton 1975a; Serong and Lill 2008).

Various models have been developed to describe the successional dynamics of vegetation communities that are relevant to the response of wet eucalypt forest communities to disturbance (e.g. Clements 1936; Egler 1954; Holling 1973; Noble and Slatyer 1980; Wilson and Agnew 1992). The theory of ‘initial floristic composition’ proposed by Egler (1954) is of particular relevance since many of the species dominant in later successional stages of the community are present in the vegetation immediately post-disturbance, having re-established as biological legacies

(seeds or sprouts) from the pre-disturbance vegetation (Purdie and Slatyer 1976; Connell and Slatyer 1977; Noble and Slatyer 1980, 1981). Nevertheless the 'relay floristic model' proposed by Clements (1936) may explain the absence of some species from one or more of the successional stages – young, intermediate or old growth – and the numerous species which differ markedly in abundance depending on time since disturbance (Hickey 1994; Turner et al. 2011).

For the purposes of this thesis, species are grouped into classes of early and late-successional plants (Huston and Smith 1987). The allocation is based here on the recorded prevalence of these species in young and older forest communities, rather than by how quickly they colonize a site after fire. The term ‘pioneer species’ is applied to those that are most abundant in regrowth forests less than 50 years since fire, most of which are known to require large gaps to germinate and grow to maturity. In contrast, the term ‘mature forest species’ is applied to those species that are more abundant in wet forest understoreys that have not been disturbed for more than 70 years. Most mature forests species are capable of occupying climax rainforest and are able in some situations (e.g. canopy gaps) to regenerate in these forests in the absence of catastrophic disturbance (Huston and Smith 1987).

The term rainforest species is distinguished from the term ‘mature forest species’ by comprising those species regularly represented within Tasmanian rainforest vegetation (*sensu* Jarman et al. 1983), and not simply adventitious within it. Jarman et al. (1983) defined rainforest as those species which occur within rainforest that are able to regenerate either vegetatively or from seed without the need for catastrophic disturbance. The rainforest species listed by Jarman et al. (1984) include at least a few among their number that are more abundant in regrowth eucalypt forest compared with mature eucalypt forest within the study region, and which are therefore classed as pioneer species for the purpose of this thesis (e.g. *Monotoca glauca*).

Tng et al. (2012) put the case that *Eucalyptus regnans* may be better classified as a fire adapted rainforest pioneer. However, traditionally this species has been placed along with other members of the genus *Eucalyptus sensu lato* as a member of the Australian autochthonous flora and not usually classified as a rainforest species. For the purposes of this thesis, *E. regnans* is considered as a pioneer species and not a

rainforest species. However, in general the analyses focus not on the eucalypts but the associated understorey species. Furthermore, rather than accepting the proposal of Lynch and Nelder (2000) to classify mixed forest as a separate vegetation community and treat it as transitional between wet eucalypt forest and rainforest, this thesis examines wet eucalypt forest as a continuum with mixed forest located on the mature forest end of the spectrum and young recently regenerated stands representing the early successional stage within the fire sere. For further discussion on the proposal by Tng et al. (2012) see Appendix 1.1 in Volume B.

Jackson (1968) developed a comprehensive model, termed 'ecological drift', for western Tasmania. This model emphasized the importance of feedbacks between the climate, topography, soil, vegetation and fire regime, such that steady states in the vegetation develop for particular combinations of factors (Wood et al. 2011; Wood and Bowman 2012). Vegetation structure and relative abundance of pioneer and rainforest plants is strongly determined by disturbance regime (Jackson 1968; Brown and Podger 1982a; Podger et al. 1988). Areas frequently or recently burned usually have an abundance of pioneer species with high light demands for establishment. The life-span of many of these pioneers are short, mostly one century or less, although individual canopy eucalypts may survive for up to 500 years (Wood et al. 2010). The abundance of pioneer species is reduced over time in the wet eucalypt forest understorey as more shade-tolerant and slower growing rainforest species (*sensu* Jarman and Brown 1983) increase in importance, eventually forming mixed forest (Gilbert 1959, Jackson 1968). Without disturbance, the eventual death of the canopy eucalypts leads to the development of cool temperate rainforest (Gilbert 1959, Jackson 1968). In fire-prone landscapes, rainforest is rare and the retention of the rainforest flora may depend on their capacity to colonize and persist in secondary wet eucalypt forests. Jackson's (1968) model is particularly relevant for explaining the distribution of vegetation types across a region and over millennia. Ashton (1981) incorporates Jackson's (1968) model in his review of the dynamics of Australia's tall wet eucalypt forests over a time-scale of decades and centuries.

There is evidence that both underlying environmental variation and the vegetation itself provides feedbacks that may maintain relatively stable boundaries between vegetation types such as tropical rainforest and savannah (e.g. Hoffmann et al. 2009;

Knox and Clarke 2012). Such relative stability has been observed between the forest and non-forest of infertile areas of Tasmania (Brown and Podger 1982a; Brown and Podger 1982b; Bowman et al. 1986; Balmer 1990; Brown et al. 2002; Marsden-Smedley et al. 2010; Wood et al. 2011; Wood and Bowman 2012). The stability between the forests and non-forest in this Tasmanian region is also supported by palynological studies across millennia (Fletcher and Thomas 2007a, b; Fletcher and Thomas 2010). However, palynological and soil profile evidence also demonstrate that major vegetation shifts have occurred in some areas providing strong evidence for Jackson's alternative stable states model (Podger et al. 1988; di Folco and Kirkpatrick 2013; Fletcher et al. 2014), and against the model proposed by Mount (1979). What remains unclear is whether there is an equivalent level of boundary stability between rainforest or mixed forest vegetation and that of wet eucalypt forest with understoreys dominated by mesophytic and sclerophyllous plants. In a study of the boundaries between warm temperate rainforest and eucalypt forest in northern New South Wales Knox and Clarke (2012) found that the boundary did not move through time, not even after severe fire. They also noted that following fire the plant communities each recovered to those resembling pre-disturbance assemblages, many species re-establishing by resprouting. Therefore evidence is mounting that disturbance patterns on their own may be insufficient to explain the stability of boundaries (Hoffmann et al. 2009; Knox and Clarke 2012; Fletcher et al. 2014).

Tng et al. (2013) sampled representative species from wet eucalypt forests, rainforest and savannah woodlands from both cool temperate Tasmania and tropical Queensland and found that data for plant traits from these species demonstrated that the wet eucalypt forests were both ecologically and functionally convergent between climatic zones and with rainforest. They argued that within the framework of alternative stable states the wet eucalypt forests occur "within the basin of attraction of rainforest" (Tng et al. 2013). If this is the case then the species representing either end of the continuum within the rainforest basin maybe more vulnerable to changes in disturbance frequency because there may be fewer feedbacks to ensure the continued occupancy of any particular part of the sere. However, in an apparent contradiction to the view point of Tng et al. (2013), both Wood and Bowman (2012) and Fletcher et al. (2014) posit that weaker feedbacks may exist which serve to hold the distribution

of wet eucalypt forests in a relatively stable state, separate to that of rainforest. The latter two studies described the dynamics within oligotrophic systems, while Tng et al. (2013) applied their hypothesis to the ecological domain of giant trees, which are not located within oligotrophic systems.

Traits such as breeding systems and dispersal distances as well as resprouting capacity are likely to influence the long-term viability of species within a fragmented landscape (McKinney 1997; Clark et al. 1999; Murray et al. 2002; Broadhurst and Young 2007; Clarke et al. 2013). Many primitive and endemic taxa are maladapted to fire and drought or have poor dispersal mechanisms but may resprout following low intensity fire (Barker 1991). These traits may make them vulnerable to population decline in response to changes in disturbance regime (frequency and intensity of logging and/or fire), habitat fragmentation and climate change (Hickey 1982; Brown et al. 1988; Barker 1992; Hickey 1994; Tng et al. 2013). Tasmanian Angiospermae and Gymnospermae species with very restricted dispersal mechanisms and which are killed by single fire events (e.g., *Athrotaxis* species) have shown substantial population declines since European settlement (Brown 1988; Cullen and Kirkpatrick 1988; Robertson and Duncan 1991). In contrast, mature eucalypts, especially thick-barked *Eucalyptus obliqua*, often survive fire and resprout from epicormic buds (Hickey et al. 1999; Turner et al. 2009). *E. regnans* has a higher mortality rate than *E. obliqua* and may be excluded if fire frequency is high (Turner et al. 2009). Ashton (1981b) provides a review of many traits which assist eucalypts and other pioneer species re-establish after fire, including seed that either survives fire in woody capsules or the soil-stored seed-bank, or which has adaptations to long-distance dispersal (e.g. the plumose seeds of Asteraceae, which are dispersed by wind).

Tasmanian wet eucalypt forests are of international conservation concern in their own right. These forests, and the present study area, include: the tallest flowering tree known on earth; immense carbon stores; and provide habitat for primitive and endemic plant species (Jarman and Brown 1983; Taylor et al. 1993; Balmer et al. 2004; Tng et al. 2012; Tng et al. 2014). Mature eucalypt trees are also critical for the perpetuation of hollow dependent fauna (Lindenmayer and Wood 2010). Recent genetic studies show the importance of Tasmanian wet forest and rainforest for conservation of genetic diversity. The fragmentation and prolonged isolation of

forests during the Pleistocene in glacial refugia such as southeastern Tasmania and parts of the present study area (Kirkpatrick and Fowler 1998; McKinnon et al. 2004), suggests there was an opportunity for regional differentiation in genetic variation. Distinctive genetic and morphological variation between northwestern and southeastern populations of several rainforest species have already been described (Barnes et al. 2000; Clark 2006). Worth et al. (2009) reports that Western Tasmania has the highest genetic diversity for *Nothofagus cunninghamii*, while Nevill et al. (2010) show similar distinctiveness in diversity at the state and regional level for *Eucalyptus regnans*.

Recent modelling has predicted climatically suitable habitat for *Nothofagus cunninghamii* will reduce by more than 90% in Victoria by 2070, making it and associated rainforest and wet forest species more dependent on Tasmania for their long term perpetuation (Worth et al. 2015).

1.4 Landscape ecology

The discipline of landscape ecology has developed over the past three decades. It integrates studies of human impacts on biodiversity with studies of natural population dynamics and variation in diversity across different spatial and temporal scales. Reviews and text books describing the discipline and methods are numerous (e.g., Brandt and Agger 1984; Naveh and Lieberman 1984; Forman and Godron 1986; Skånes 1997; Gergel and Turner 2002; Collinge 2009). The expansion of landscape ecology has been enabled by technological advances in areas such as: geographic information systems, remote sensing, global positioning systems, internet, and computer technology. Together these have made it possible to access, manipulate and model increasingly high-resolution data for large geographical regions to determine the landscape-scale impact of humans on gene flow, distribution and abundance of species, communities and ecosystems.

Among the many concepts and models within the discipline of landscape ecology is Island Biogeography Theory (MacArthur and Wilson 1967), which relates the size of islands and their isolation from other land areas to species colonization and extinction rates. This model has been generalised to explain the effects of landscape

fragmentation on meta-population dynamics and biodiversity (Levins 1969; Saunders et al. 1991, 1999). In landscape ecology, 'habitat fragmentation' is the term often used to describe the process anthropogenic landscape modification such as vegetation clearance, which results in the development of non-contiguous remnants of native habitat patches. The term 'habitat' is used to describe the environment suitable for use by a particular species (Lindenmayer and Fischer 2006). The term 'matrix' is used to describe the land cover type with the greatest area within the landscape, which in most fragmentation studies is usually represented by the most disturbed land cover type such as agricultural land or urban areas (Lindenmayer and Fischer 2006). In Island biogeography theory, a patch, like an island, is defined as an area of native land cover, surrounded by a matrix of land or water. Within many studies the landscape is classified and mapped into two types of land cover: habitat and matrix. For such situations, island biogeography theory suggests that patch size, habitat heterogeneity within the patch, and patch isolation may be strong influences on local species richness (MacArthur and Wilson 1967; Saunders et al. 1991, 1999). Hence habitat fragmentation and configuration patterns caused by vegetation clearance or other anthropogenic disturbance may influence and change individual species distributions (Noss and Harris 1986; Noss 1987).

The limitations of Island Biogeography Theory for ecological predicting biodiversity responses are now well documented (Gascon and Lovejoy 1998; Lindenmayer and Fischer 2006; Laurance 2008; Le Roux et al. 2015). For example the edges of habitat areas juxtaposed to cleared land are often subject to a myriad of processes and influences collectively referred to as edge effects (Gascon and Lovejoy 1998). These include the greater probability of weed invasion from agricultural or urban land, increased browsing pressure, predation from introduced animals (e.g. cats), nutrient enrichment from fertiliser drift, pollution, exposure to more extreme micro-climatic variation etc (Saunders et al. 1991). The variability of patch habitat quality, including structure, and the potential variation in species use of, or ability to move through, the matrix may impact more on species mortality and colonization rates than patch size and isolation in some circumstances (Lindenmayer and Fischer 2006; Laurance 2008; Le Roux et al. 2015). In particular the qualities of the surrounding landscapes,

including the abundance of particular habitat types and heterogeneity may all influence the probability of a species occurrence or abundance at the site.

The term 'landscape context' (LC) is defined for the purposes of this thesis as the vegetation or land area surrounding a site, including both habitat and matrix in the surrounding area (*sensu* Noss and Harris 1986). The realisation that LC may influence species distribution has resulted in an explosion of studies in landscape ecology (Henle et al. 2004), but mostly in fragmented or relictual landscapes (*sensu* McIntyre and Hobbs 1999) dominated by cleared land. These have investigated the effects of both reduced habitat area and fragmentation associated with land clearance (McGarigal and Cushman 2002; Fahrig 2003; Collinge 2009).

Habitat fragmentation is associated with several processes including reduction in total habitat, decreasing patch size, increasing isolation of patches and an increase in the ratio of the patch that is subject to edge effects (Saunders et al. 1991; McIntyre and Hobbs 1999; Saunders et al. 1999). Hobbs and McIntyre (1999) developed a model which describes commonly observed steps and processes in converting natural ecosystems (including habitat) into areas of anthropogenic land-use such as agricultural or urban land. It distinguishes thresholds in landscape conversion commencing from the 'intact' landscape in which more than 90% of the area is occupied by largely unmodified native vegetation. At the other end of the scale are '*fragmented'* landscapes, distinguished as those in which there is less than 60% native vegetation cover, at least some of which is still unmodified. In contrast the few remaining native vegetation patches in '*relictual'* landscapes are usually highly modified. Importantly Hobbs and McIntyre (1999) distinguish an intermediate '*variegated'* landscape stage in the evolving conversion of landscapes. In this stage native vegetation occupy more than 60% of the landscape but vary in their quality as a consequence of modification processes associated with surrounding land use change. Such modifying processes may include silviculture and fire regimes, both known to impact on biodiversity. In this thesis, the term landscape fragmentation is also applied to disturbance processes that result in the conversion of mature forest to regrowth forest.

Given the strong association of fragmentation processes with multiple processes including habitat loss, isolation, habitat change, and edge effects, it is inevitably challenging for scientists to distinguish between the which of these processes is responsible for observed biological responses. A large number of metrics have been devised to measure the various properties of habitat patches and landscapes that may impact on biodiversity, and the software package FRAGSTATS produced to assist with generating these (McGarigal and Marks 1995; McGarigal et al. 2002). However many landscape characteristics, and the metrics describing them are strongly auto correlated potentially confounding the results of many studies (McGarigal and Cushman 2002; Smith et al. 2009; Thornton et al. 2011; Mairota et al. 2015). Distinguishing between the separate effects of the various processes that accompany landscape modification and fragmentation may be critical to mitigating against these impacts (Lindenmayer and Fischer 2006). Fahrig (2003) reviewed 100 fragmentation studies and found that most were patch-scale rather than landscape scale studies and most designs were unable to distinguish patch size effects from the other effects of fragmentation. Because many studies fail to distinguish the effects of habitat loss from other processes of fragmentation, and because the term fragmentation is often applied to all the associated processes, Lindenmayer and Fischer 2006 have suggested the use of the term 'habitat sub-division' to distinguish the process of separating a single large habitat area into several smaller areas.

The landscape fragmentation literature, is generally applied to the study of impacts on biodiversity associated with anthropogenic landscape modifications, usually landscapes which are fragmented by clearance or conversion to plantations (Lindenmayer and Fischer 2006). However, it also encompasses studies in regions of native vegetation where anthropogenic modification processes have led to the loss or sub-division of a particular habitat types such as late-stage or oldgrowth forest types, as a consequence of timber harvesting, or anthropogenic alterations to fire regimes (Lindenmayer and Fischer 2006). Modifications to fire and grazing regimes are usually associated with or precede intensification of land use and land clearance and impact on species dynamics and populations (Hobbs 1987; Syphard et al. 2007).

Spatial and temporal variation in the natural environment, including climate and natural fire regimes, has led to naturally strong spatial patterning in habitats

(Lindenmayer and Fischer 2006). This patterning has had a profound influence on the evolution of species and is likely to contribute significantly to explaining natural species distribution and richness patterns (e.g. Haig et al. 2000; Dullinger et al. 2011; Frey et al. 2012).

Distinguishing the effects of natural environmental variation including natural fragmentation patterns from those of anthropogenic habitat fragmentation on species responses provides another challenge for empirical studies that should also not be overlooked (Lindenmayer and Fischer 2006). Landscape fragmentation is not random but often targets particular habitats and environments leading to a confounding between natural environmental variation and landscape metrics.

In the landscape fragmentation literature there has been an increasing tendency to view landscapes as a mosaic of different types of patches based on the approach of Forman (1995) or as a continuum of habitat suitability (Manning et al. 2004; Fischer et al. 2004; Lindenmayer and Fischer 2006; McGarigal et al. 2009). Patches are often defined more specifically as a relatively homogenous, non-linear area, of habitat (Lindenmayer and Fischer 2006). In such studies different habitat types may be more narrowly defined in terms of a specific characteristic, for example, dominance by a particular life form, age-class or species that make it suitable for a particular focal species or species group. The patch is often distinguished from corridors. Corridors being linear extents of habitat that are connect two or more patches (Lindenmayer and Fischer 2006). These may assist some species move between patches in the landscape but due to their narrowness, corridors are often unsuited to more continuous occupation by the focal species and do not provide core habitat.

The landscape fragmentation literature is immense and still growing (Lindenmayer and Fischer 2006). Several reviews and syntheses of the effects of landscape fragmentation have been published (e.g. Saunders et al. 1991; Mazerolle and Villard 1999; Debinski and Holt 2000; McGarigal and Cushman 2002; Fahrig 2003; Hobbs and Yates 2003; Aguilar et al. 2006; Bennett et al. 2006; Lindenmayer and Fischer 2006; Collinge 2009; Swift and Hannon 2010; Thornton et al. 2011; Humphrey et al. 2015). However there has been a bias towards vertebrate animals, particularly birds, more studies targeting threatened species compared with more common taxa, and few

studies being multidisciplinary (Debinski and Holt 2000; McGarigal and Cushman 2002; Fahrig 2003; Collinge 2009). This bias is not restricted to the landscape fragmentation literature but has been reported more generally within the published biological literature (Fazey et al. 2005).

Debinski and Holt (2000) reviewed 20 studies and concluded that although there were inconsistencies between results, most supported the theory that "movement and species richness are positively affected by corridors and connectivity, respectively" (Debinski and Holt 2000, p 342). Likewise, Bennett et al. (2006) reviewed empirical fauna studies that investigated the nature conservation implications of landscape fragmentation for within agricultural landscapes. They concluded that the properties of agricultural land mosaics (extent, composition and configuration) all strongly influence the occurrence of fauna, but they observed that the responses varied greatly. An example of a result from a landscape mosaic study in Victoria, Australia, demonstrated that of the landscape attributes examined tree cover accounted for 55% of the variation woodland bird species richness among landscapes (Radford et al. 2005). Another Australian bird study, not included in the review by Bennett et al. (2006), provided evidence that 50 percent of the bird species studied within riparian habitats had abundance responses related only to variation in LC while 80% responded to the combined effects of local site condition and LC (Martin et al. 2006).

A review by Swift and Hannon (2010) of 17 fauna and one fungi study similarly demonstrated LC effects on species responses. However, this review also demonstrated that most species tend to show a non-linear response to landscape fragmentation, with most responses occurring only after a critical threshold in habitat loss had occurred. The investigation of critical thresholds at which species respond to both habitat loss or fragmentation is therefore another important aspect of the fragmentation literature (e.g. Villard and Metzger 2014).

Swift and Hannon (2010) also noted that a temporal lag often occurred between landscape change and species responses. Factors potentially influencing the response of species to habitat sub-division include the total amount of habitat available and the quality or 'resistance' of the matrix for species movement and survival (Fahrig 2001).

Such non-linear responses and temporal lags add to the difficulty in detecting LC effects on biodiversity.

A review of results for 954 fauna species from 122 focal patch studies was undertaken by Thornton et al. (2011) from which a diverse range of taxa were also found to respond to LC, patch-size and within patch heterogeneity. Among fauna groups they observed that mammals were particularly sensitive to their LC. They also noted that the probability of detecting landscape responses was influenced by study methods, choice of response variable, sample size and choice of landscape metric (Thornton et al. 2011). They noted that few studies tested for spatial autocorrelation within their data sets, or correlations among the predictor variables. They noted that this oversight could be leading to erroneous conclusions about the nature of species relationships with their environment, a concern raised by other researchers (Betts et al. 2006; Cushman et al. 2008; Smith et al. 2009).

The development metrics, and the problems associated with the scale of landscape responses have also been the focus of several studies (Neel et al. 2004; Cushman and McGarigal 2008; Cushman et al. 2008). Although Thornton et al. (2011) found no evidence among the studies they reviewed of a sensitivity in the response of fauna to multiple buffer scales, they nevertheless recommended the use of multiple buffers for the generation of LC variables citing the results demonstrating sensitivity to landscape radius from a simulation study by Moilanen and Nieminen (2002). Other studies have also suggested species vary in the scale at which they are sensitive to landscape effects (Chust et al. 2004). For example, Steffan-Dewenter et al. (2002) found that the abundances of solitary wild bee species were associated with differences in the proportion of native vegetation present in the surrounding areas measured up to distances of 750 m radius; but honey bees were associated only with landscape differences measured at larger radial landscape distances. Differences among species response to scale of landscape patterns increase the difficulty of detecting LC influence.

Many of the results from fragmentation studies undertaken in southeastern Australia prior to 2005 have been reported within the synthesis provided by Lindenmayer and Fischer (2006) on the subject of landscape fragmentation and habitat change. Among

these are some of the results coming out of the Tumut long term experimental project studying eucalypt forest remnants within a matrix of pine plantations, at Wog Wog, New South Wales (Margules 1992; Margules 1996). This area was fragmented experimentally by the conversion of eucalypt forest to *Pinus radiata* plantations. Lindenmayer et al. (1999) reported no association found between abundance of individual mammal species and LC or remnant patch size. In contrast, Lindenmayer et al. (2000c) found mammal assemblages were impoverished in remnants compared with areas of continuous eucalypt forest and that species richness increased with remnant patch size. Even small remnants were able to be occupied by a greater number of vertebrates species than anticipated, while some native species were located with the radiata pine stands, although their presence in the matrix may have been associated with proximity to remnant eucalypt stands (Lindenmayer and Fischer 2006).

Of the vascular plant studies undertaken at the Tumut long term experimental site, the first finding reported was that common plants constitute more of the flora in small remnant native vegetation patches (0.25 ha) compared with either large patches (3 ha) or intact forest, a difference attributed to the greater environmental change in the smallest remnants (Morgan and Farmilo 2012). Small remnants (0.25 ha) also contain a higher species densities when measured at small spatial scales (1 m^2) and medium spatial scales (16 m^2) compared with intact forests but not at the largest spatial scale of sampling (144 m^2). However, species densities did not differ between larger patches and intact forest for any sample size (Farmilo et al. 2014). The differences observed in small patches were attributed to the greater influence of pine plantation to microclimate, and soil moisture characteristics (Farmilo et al. 2013; Farmilo et al. 2014).

Fragmentation studies were established earlier in Amazonia than Australia and have revealed much more about the landscape ecology of vascular plant species for tropical forest ecosystems. Results there provide evidence that forest fragmentation by clearance influences tree species composition and forest structure at the edge of tropical forest remnants, causing mortality in large canopy and emergent trees and associated losses in above-ground biomass (Laurance 1991; Ferreira and Laurance

1997; Laurance et al. 1998b; Laurance et al. 1998a; Mesquita et al. 1999; Laurance et al. 2000; Laurance et al. 2003; Laurance et al. 2006).

Although long term experimental fragmentation studies and simulation studies enable greater capacity to distinguish between the various processes of landscape fragmentation, a growing number of empirical studies have demonstrated that plant responses often lag well behind landscape change (Tilman et al. 1994; Vellend et al. 2006; Cousins 2009; Koyanagi et al. 2012; Rigueira et al. 2013; Bagaria et al. 2015). The lag time, which is referred to within Island Biogeography Theory as the relaxation time, contributes to what is termed an 'extinction debt' or 'colonization credit' within the biodiversity of patches that have not reached equilibrium with their current landscapes. Evidence that some plant species patterns are better explained by historical landscape patterns than current patterns have been provided by studies in both European grasslands (Lindborg and Eriksson 2004; Reitalu et al. 2009; Cousins 2009; Piqueray et al. 2011; Koyanagi et al. 2012; Bagaria et al. 2015) and temperate forest and woodlands in Europe and northern America (Östlund et al. 1997; Gerhardt and Foster 2002; Verheyen et al. 2003; Graae et al. 2004; Vellend et al. 2006; Verheyen et al. 2006; Kimberley et al. 2015). These studies suggest that variation in life history, reproductive and dispersal traits contribute to species vulnerability to extinction and therefore also the rate at which plant species distribution, abundance and associated plant species richness patterns respond to landscape change. The observation that many life-history traits co-vary across species has led to the concept of the fast-slow continuum hypothesis (Franco and Silvertown 1996). Species with slow metapopulation dynamics, defined as those with both low rates of colonization and extinction, are likely to be slow to respond to such landscape changes due to characteristics such as long life spans or the capacity to reproduce vegetatively (Vellend et al. 2006). Some slow forest herbs have been identified as having particularly slow migration rates with a high risk of extinction unless habitat connectivity is maintained (Matlack and Monde 2004).

Despite the complications of a lag in plant responses to landscape change, more than half of the European plant studies incorporated within a review of woodland fragmentation found evidence of positive associations in richness or plant occurrence with woodland patch size, proximity to other patches, ecological continuity, and patch

quality (Humphrey et al. 2015). One study in Italy found a linear increase in perennial herb richness up to a patch size of 35-40 ha (Digiovinazzo et al. 2010), whereas a study of forest plants in Belgium found an association with forest age but no association with current patch size (Honnay et al. 1999). When the distributions of 59 individual species were analysed in Belgium woodlands 34 were found to be associated with three or more landscape metrics including patch size (Jacquemyn et al. 2003). Vellend et al. (2006) observed that Belgium woodlands, which have become fragmented only since 1775, had higher than expected richness levels of 'slow species' based on models of richness to patch area developed for long fragmented landscapes in England.

Aguilar et al. (2006) reviewed the effects of landscape fragmentation on reproductive success in plants (fruit or seed production) for 89 animal pollinated plant species from 53 studies and found that on average fragmented landscapes were associated with reduced reproductive success in most of the plant species studied. The negative response to landscape fragmentation was much stronger among obligate out-breeder (self-incompatible) species, where as the difference in reproductive success in species that were self-compatible could not be detected. In contrast, there was no evidence that the number of animal pollinators available to the species or its life form affected reproduction in response to landscape fragmentation (Aguilar et al. 2006). They noted that species capable of being pollinated by introduced honey bees (*Apis mellifera*) were often less affected or benefited from landscape fragmentation in regions where these honey bees were common.

Given the wide variation in plant traits including life history, longevity, reproductive systems and dispersal mechanisms, it is no surprise that many studies have shown no association between individual plant species, plant richness and community assemblages and some LC factors such as patch size (e.g. 6 out of 14 studies found plant richness in European woodlands was not associated with patch size, Humphrey et al. 2015). In Tasmania, Woolley and Kirkpatrick's (1999) vegetation study investigated the condition and geometric configuration of remnant forests on plant species composition in northern Tasmanian basalt landscapes. The study showed that floristic composition and vegetation condition were associated more strongly with

vegetation type and management regimes than to patch size or time since the patch had become isolated.

Despite the varied results of landscape studies there is now overwhelming evidence from numerous empirical and theoretical work that land clearance and fragmentation increases the vulnerability of some species to population decline and local extinction (Saunders et al. 1991; Turner 1996; Fahrig 2001; Collinge 2009). These studies conclude habitat maintenance is critical for biodiversity conservation (Fahrig 1997).

Given the importance of LC for biodiversity in regions fragmented by vegetation clearance, there is also a growing interest in understanding the implications for biodiversity of age class distributions in regions subject to landscape scale wildfires. A desire to determine the impact of management burning and wildfires on conserving biodiversity with reserve areas has led to a major multidisciplinary study of LC influences on fauna within the mallee ecosystems of southeastern Australia. Of 28 bird species sufficiently common across 26 sites studied the distribution and abundance of 14 of these birds were strongly associated with at least one LC metric (Taylor et al. 2013). Few birds shared similar responses to LC, most models demonstrating different preferences among species. However, there were no species that were associated with areas with landscapes dominated by very young fire ages. Only three birds were strongly associated with sites having landscapes dominated by older vegetation (>35 years) at both the site and landscape scale. The authors used the models to predict outcomes for particular bird species, but no strategy provided the best outcome for all species (Taylor et al. 2013). The associated study of reptiles in the same region demonstrated that the maximizing fire ages diversity in the landscape was not associated with an improvement in reptile diversity either at the alpha, beta or gamma level. Optimal beta diversity in reptiles was maximized in landscapes with a high proportion of long unburnt vegetation but at sites within such landscapes alpha level of diversity in reptiles was reduced cancelling out any benefit for gamma diversity (Farnsworth et al. 2014).

The impacts of recent wildfires within southeastern Australian wet eucalypt forests has been severe in the last two decades. Lindenmayer et al. (2013b) reported on the relative impact of fire severity at both the site and in the surrounding landscape as

well as the availability of hollow-bearing trees needed for nesting for four arboreal mammals. Both the sugar glider (*Petaurus breviceps*) and the endangered leadbeater's possum (*Gymnobelideus leadbeateri*) were rarely located in burned forest areas, whereas the mountain brushtail possum (*Trichosurus cunninghami*) and the greater glider (*Petauroides volans*) were found in both burned and unburned forest sites. The greater glider was negatively associated with the severity of fire at the site level but mountain brushtail possum's was least common in sites burned only at moderately. All four species were positively associated with hollow-bearing trees and all but the mountain brush-tail were negatively associated with the amount of burned forest in the surrounding landscapes (Lindenmayer et al. 2013b). Within the same wet eucalypt forest region Lindenmayer et al. (2014b) reported that the majority of bird species studied also responded to landscape-level fire severity. Only one species, the red flame robin, showed a positive association with the amount of burned forest. Although other species were generally negatively associated with the amount of forest burned in their landscape they varied more widely in their responses to the amount of severely or moderately burned forest. However, the detection rates for at least one species, the brown thornbill, were recovering after just two years and were more likely to be found in areas that they had been detected prior to the fire (Lindenmayer et al. 2014b). The effects not only of wildfire, but also climate change on biodiversity, highlight the importance of ensuring that natural refugia from wildfire and climate change be protected and buffered from the effects of other anthropogenic disturbance influences such as timber harvesting and developments (MacKey et al. 2012). Statistical landscape modelling for wildfires have been developed to identify such refugia (Berry et al. 2015).

Societal pressure is increasingly demanding that silvicultural management not only ensure a sustainable level of timber production but that harvesting practices will not jeopardise the survival of native biota (Mitchell and Beese 2002). To this end many researchers have been specifically investigating the impacts on biodiversity from fragmentation and landscape change caused by timber harvesting (e.g.Franklin and Forman 1987; Li et al. 1993; Smyth et al. 2005; Franklin and Lindenmayer 2009; Gustafsson et al. 2012; Baker et al. 2013c; Baker et al. 2013a; Baker et al. 2013b; Fedrowitz et al. 2014; Baker et al. 2015; Fountain-Jones et al. 2015). The many

findings include: reduced harvest area can reduce impact on adjacent unharvested areas while increasing the positive influence from mature forests on regeneration at the site (Baker et al. 2013a; Baker et al. 2013b; Baker et al. 2015); that the preservation of biological legacies within harvest sites, such as are often retained after natural disturbance, can mitigate harvesting impacts for many species (Franklin et al. 2002).

A study in a production forest landscape in the Oregon Coastal Range demonstrated that both vegetation type in the sampled plot and vegetation communities in the surrounding landscape explained the observed pattern in bird communities, but that many late-seral bird species were generally more abundant at sites with more heterogeneous landscapes rather than those that were least fragmented by timber harvesting (McGarigal and McComb 1995; Cushman and McGarigal 2004a). There was also no decline observed in the abundance or richness bird species in association with the reductions in the size of remnants of oldgrowth montane forests in a matrix of silvicultural regrowth on Vancouver island, Canada (Schieck et al. 1995). Studies of another late-seral bird species of North America, the Brown Creeper (*Certhia americana*), have demonstrated several scale-related landscape effects from harvesting that impact on this species (Poulin and Villard 2011; Poulin et al. 2008; D'Astous and Villard 2012): a positive association between nest occupancy and density of snags and large-diameters of trees at a radius of 80 m; a positive association between nest occupancy and the presence of mature forest at scales of 250 m radius; negative association between nestling success with distance from edge of cone-producing plantations up to a threshold of 100 m due to increased predation; in an experimental selection harvest site where nest substrates invertebrate assemblages and biomass per unit area were the same partial harvesting treatment still reduced nest densities by 50%, an impact caused by the additional effort required for food delivery due to the reduced density of foraging substrates at harvested sites.

Perhaps the most publicised issue for forest management in the Pacific northwest Forests of north America is the management of northern spotted owl, a threatened species dependent on old growth habitat for nesting and which is extremely sensitive to disturbance by harvesting. LC studies have demonstrated that the species: requires greater than 35-40% mature forest habitat in the landscape, is unable to utilise areas

with hard edges present in the immediate 3 ha landscape, will use 50-800 ha landscapes containing hard edges, is not sensitive to diffuse natural disturbance edges even within landscape areas of <3 ha; extinctions were more likely and colonization less likely in the presence of a competing species and colonizations were (Dugger et al. 2011; Marcot et al. 2013; Comfort et al. 2016).

Although the response of biodiversity to LC change is highly variable it is likely as the total habitat declines that species will become extinct. Already large areas of Australian forest have already been cleared, accruing an extinction debt that remains largely ignored, and certainly uncalculated. Continuing resource extraction and clearance is inevitable if human populations continue to grow. Mitigation of this impact is reliant on identification and protection of refuges; targeted habitat restoration; and maintenance of critical thresholds of habitat, appropriately configured. This requires the development of landscape metrics and planning tools such as maps at the appropriate scale and resolution that can be used by landscape managers and planners.

1.5 Potential LC responses by wet forest plants

Within the model framework provided by alternative stable states, it is possible that one of the stabilizing factors preventing major shifts in vegetation type is the influence of LC. The dependence of successional processes on spatial proximity to seed sources, and moderating influences of adjacent vegetation may be critical in limiting vegetation change.

According to the classical relay floristic model of plant community succession, disturbed sites are likely to be relatively inhospitable to species of climax communities and are initially colonized by light demanding pioneer species (Clements 1936). The light demanding pioneer species serve to modify the site environment facilitating colonization by less light demanding species, which over time out-compete and replace the initial pioneers. In this manner the composition changes in relay fashion, with each phase in the succession characterised by a different group of species. Connell and Slatyer (1977) distinguished this successional pattern as the

facilitation pathway. If floristic composition of wet eucalypt forest changes through time in such a relay fashion, then it is likely proximity to mature forest will not be important until prior occupancy by pioneer species has modified the site sufficiently to facilitate colonization by mature forest species. It might be expected that once the minimum condition for mature forest species occupancy has been reached, that proximity to mature forest will then influence successional dynamics until the propagule sources of each late stage species become available within the patch, rendering external sources less influential. In these circumstances young forests may not show evidence of mature forest influence, and older forests would be influenced by current landscapes not those of the past.

Egler (1954) agreed that relay floristics provided a valuable model for primary succession and that sites recovering from secondary disturbance generally have phases in succession characterised by the dominance of particular species groups. However he described an alternative model for when species of later successional phases do not require facilitation by other species in order to colonize. In this case he suggested that the majority of species in the later successional stages will comprise a subset of species within the initial floristic composition. However, Egler's (1954) 'Initial floristic composition' model has been interpreted in different ways (Wilson et al. 1992; Wilson 2014).

One interpretation of the 'Initial floristic composition' model, clearly stated by Egler (1954), was that species present in all successional phases may be present from the outset. This follows from observations by many authors (including Clements) that among plant species common to later-stage communities, many are able to survive disturbance either vegetatively or as seeds and are therefore present in the colonizing community (Wilson 2014). Connell and Slatyer (1977) distinguish this interpretation of Egler's model as an example of a tolerance pathway, since the later stage species do not require prior facilitation in order to occupy the site. In this interpretation the pre-disturbance community may have a strong influence on the establishment of the post-disturbance community and it is likely that the vegetation will return to a composition strongly resembling the pre-disturbance community, if for no other reason than their presence demonstrates a general adaptation to the local environment. In situations where the pre-disturbance community has a particularly strong influence on the

composition of secondary forest after disturbance then it is to be expected that LC influence will be correspondingly weak. It is also expected that whatever weak LC influence there is would be evident even in young communities and therefore that there is likely to be a legacy effect of LC patterns following fire evident in the composition of older communities, although ongoing LC influence may also result in compositional association with current LC patterns as well.

In another interpretation of Egler's model, early colonists might be predictors of later communities by virtue of their competitive advantage over species arriving later, regardless of whether they were legacies from the pre-disturbance community or arrived from sources external to the site (Wilson 2014). Connell and Slatyer (1977) coined this successional trajectory the 'inhibition pathway'. This concept has been developed in greater detail, as part of competitive exclusion theory (Tilman 1990; Waters et al. 2013). If this pathway is important in wet eucalypt forest successional dynamics then it might be expected that proximity of mature forest patches would be most critical in its influence on community succession in the initial phase of colonization and later changes in LC patterns would have little or no influence over the community.

1.6 Knowledge Gap

In the last decade, while landscape fragmentation studies have become more numerous, the bias towards single-species faunal studies has remained. Among plant studies investigating fragmentation effects in Australia, a few have focused on impacts on breeding systems (Rossetto et al. 2004a; Rossetto et al. 2004b; Krauss et al. 2007; Mimura et al. 2009; Breed et al. 2012; Gauli et al. 2013), and more have investigated the effects on species abundance within remnant patches (Woolley and Kirkpatrick 1999; Saunders et al. 2003; Debuse et al. 2009; Morgan and Farmilo 2012; Farmilo et al. 2013; Kooyman et al. 2013; Farmilo et al. 2014). In common with most landscape ecology studies, these studies have explored the effect of fragmentation in polarised landscapes and focused on the biodiversity within forest or woodland remnants within agricultural, plantation or urban landscapes. The effects of fragmentation within native forest by disturbance such as wildfire and timber harvesting have been the focus of few empirical plant studies.

Among forest plant studies in areas of predominantly native vegetation, there is one that studied the effect of isolation between secondary forest communities in tree fall gaps in tropical forests of Amazonia (Grau 2004) and one that studied the landscape effects on recovery of vegetation following fire in Yellowstone National Park (Turner et al. 1997). In another study within the USA, the distance from old growth forests was found to be important in determining the establishment success of various plant species within the understorey of secondary regrowth forests (Matlack 1994a). Baker et al. (2015) found that vascular plant assemblages within five to eight year old silvicultural regrowth in Douglas-fir dominated forests were more responsive to distance from the edge of forest aggregates retained during timber harvesting operations than communities of ground active beetles or spiders and harvestmen. Their study also showed that within older silvicultural regrowth (21–26 years old) assemblages had recovered within the harvested areas to such an extent that this variation with distance was much less apparent. A similar study in Tasmania by Tabor et al. (2007) demonstrated that four rainforest tree species declined in frequency with distance away from mature forest edge at five regrowth forest sites.

To my knowledge, at the commencement of this study, there was no study previously published on the effects of landscape upon the floristic variation in Australian wet eucalypt forests within landscapes dominated by other native eucalypt forest apart from the study by Tabor et al. (2007). Furthermore, the importance of LC influence on the successional dynamics within wet eucalypt forest has not previously been the focus of empirical study using a chronosequence approach.

"... Everything is influenced by the wilderness of the rugged landscape. With each step, one encounters the beauties of unspoilt nature, with signs of decrepitude; trees reaching a very great height, and of a corresponding diameter, are devoid of branches along the trunk, but crowned with an everlasting green foliage. Some of these trees seem as ancient as the world, and are so tightly interlaced that they are impenetrable. They support other trees of equal measurement which fall from old age, and nourish the soil with their decaying fragments. Nature, in all its vigour, and at the same time in decline, offers to the imagination something more imposing and picturesque than the sight of this same nature embellished by civilised man's industry. In wishing to conserve only its beauty, man has managed to destroy its charm, and ruin its exclusive character—the one of being always old, and always new."

Description of the Port du Nord (Recherché Bay), southern Tasmania, in May 1792, from the published diaries of Antoine Raymond Joseph de Bruni, chevalier d'Entrecasteaux (1737–1793), translated by Duyker and Duyker (2001).[3]

[3] Duyker, E. and Duyker, M. eds (2001) Van Diemen's Land (Chapter IV) **In**: Bruny d'Entrecasteaux: Voyage to Australia and the Pacific, 1791–1793. Melbourne University Press, Melbourne, p 34.

Chapter 2 Landscape context variation, 1947–2009

2.1 Abstract

Meta-population theory has established that species presence and abundance within a site is not only related to the environment within at a site but also to the influence of the surrounding landscape, i.e. its landscape context (LC). Habitat suitability for species may also be related to its seral development and historical disturbance frequency, referred to here as landscape stability. Since each vegetation type is associated with a distinctive disturbance range, relative stability scores were assigned to each vegetation type from a scale of 0.5 (most frequently and severely disturbed) to 10 (rarely disturbed). A simple metric, the Landscape Context Index (LCI) was developed to provide a relative measure of the vegetation stability in the surrounding area by calculating the weighted average of stability scores for each landscape. The LCI metric was used to measure changes in LC in a native forest region used for timber production between 1947, 1985 and 2009. Timber harvesting was associated with a greater loss in vegetation stability than occurred in response to wildfires over the two periods measured within the study area, and more of the landscapes within the region were associated with a reduction in LCI scores than increased in LCI score as a result of vegetation aging in undisturbed areas. Nevertheless, the metric also demonstrated that the introduction of the Forest Practices Code in 1985 has led to some mitigation in the reductions in LCI scores from timber harvesting. Practices that contributed to reducing landscape disturbance impacts included the reduced aggregation and size of clearfell coupes. However, there was an intensification of wood production in eastern areas where timber plantations were established after the Regional Forest Agreement which led to further reductions in LCI metric scores in eastern areas, which had already been heavily impacted by agricultural development, a long history of timber harvesting and wildfires.

2.2 Introduction

The abundance of many species is not only affected by their local environment but also the nature of the surrounding landscape (Saunders et al. 1991; Fahrig 2003;

Collinge 2009). Landscape context (LC) has been defined as 'the surrounding habitat matrix and corridors' (Noss and Harris 1986; Noss 1987). The most important influence of LC may be on the resilience of species to disturbance (Lindenmayer and Fischer 2006; Lindenmayer and Hobbs 2007).

The majority of empirical studies documenting the ecological relationship between LC and species or biodiversity have been undertaken in fragmented or relictual landscapes (*sensu* McIntyre and Hobbs 1999); landscapes with little remaining native habitat (Collinge 2009). In many LC analyses land is treated as cleared or uncleared (e.g. Michaels et al. 2010), ignoring variation in habitat quality within uncleared areas. Nevertheless, recognition of variation in habitat quality has been increasing in studies of LC. Haslem and Bennett (2008) measured LC using the amount of native vegetation cover as well as the richness of different vegetation elements. Radford and Bennett (2007) classified landscapes along a mapped gradient of tree cover. They further separated them according to tree aggregation. Steffan-Derwenter et al. (2002) distinguished differences in LC based on the proportion of each mapped vegetation type in the surrounding landscape. McGarigal and McComb (1995) used ratios of successional stages in their calculation of LC. Another metric developed by Brown and Vivas (2005) quantifies LC in terms of a disturbance gradient. While Brown and Vivas (2005) base disturbance on non-renewable energy inputs most suited to landscapes differing markedly in such energy inputs, their methodology could be modified to measure LC for other gradients. Such a LC metric is relevant to biodiversity conservation in situations where there is a strong biotic link between disturbance history and the successional stages in vegetation development, as in the production forests located within the perhumid climatic zone of Tasmania.

Lindenmayer and Fischer (2006) provide several examples of landscape evolution studies that document the process of habitat loss as settlement expands in frontier[4] regions. Most document the transition resulting from clearance/ deforestation of natural areas and conversion to agricultural land uses and urban settlement, a process

[4] The term frontier is used here to mean the hinterland between areas settled by industrialised people and natural areas relatively free from modern development.

which often commences with timber harvesting (e.g. Ferraz et al. 2005). Although fewer in number, there are also landscape histories that focus on disturbance regime changes and associated alterations in LC patterns caused by harvesting within regions of native forest (e.g. Covington and Moore 1994b; Delacourt and Delacourt 1996; Hessburg et al. 2000; Broadbent et al. 2008). Such studies usually investigate the ratio of core to edge resulting from logging, since numerous studies have demonstrated harvesting edge-effects impact biodiversity of remaining forest (Forman and Moore 1992). Simulation modelling has demonstrated that timber harvesting may have significant and long-lasting impacts on LC patterns (Franklin and Forman 1987; Li et al. 1993; Spies et al. 2007). Changes in technology, culture, regulation, markets and climate can affect patterns of disturbance in frontier forests, thereby causing perceptible change in overall LC (e.g. Merry et al. 2006). The capacity to affect LC patterns through regulation and management of disturbance is important given the mounting evidence that LC, including landscape structure (Tischendorf and Fahrig 2000a, b), is able to influence the persistence and abundance of many indigenous and exotic plants and animals (Baker et al. 2013b), and the ecosystem services that they collectively contribute (Turner et al. 2013).

This chapter provides a largely descriptive account of the landscape variation within the study area[5] within Tasmania's Southern Forests (Figure 2–1) where data analysed for this thesis was collected. After a brief overview of the land use history (section 2.3), this chapter reports on:

- how the study area fitted within the habitat fragmentation framework proposed by McIntyre and Hobbs (1999) for the years 1947, 1985, and 2009 (See section 2.5.1.1;) and
- what changes in vegetation have occurred within it over time (i.e. between1947 to 1985 and 1985 to 2009)? (See section 2.5.1.2.)

[5] Although the study area was confined to areas below 600 m altitude and which received a minimum of at least 1000 mm of mean annual rainfall, the landscapes which surrounded parts of the study area included some adjacent areas that were above 600 m altitude or receiving below 1000 mm in mean annual rainfall.

The chapter then analysed the LC variation within the study area using a new metric based on the approach of Brown and Vivas (2005) to determine:

- what spatial and temporal LC patterns were present within the study area? (See section 2.5.2.1;)
- how much it varies within and between each vegetation community over time? (See section 2.5.2.2;)
- how much variability there was in LCI metric score in the study area and what evidence was there of auto-correlation in LCI scores between scales and over time within the study area and how this was affected by patch size? (See section 2.5.2.3;) and

Finally, this chapter examines the relationship between changes in disturbance history and LCI scores in order to determine:

- to what extent timber harvesting has been responsible for the observed changes in LCI compared with other types of disturbance? (See section 2.5.3;) and
- to what extent have changes in industrial practice, forest policy and regulation resulted in differences in coupe size and aggregation and how has this changed LCI score in response to timber harvesting? (See section 2.5.4.)

2.3 The study area

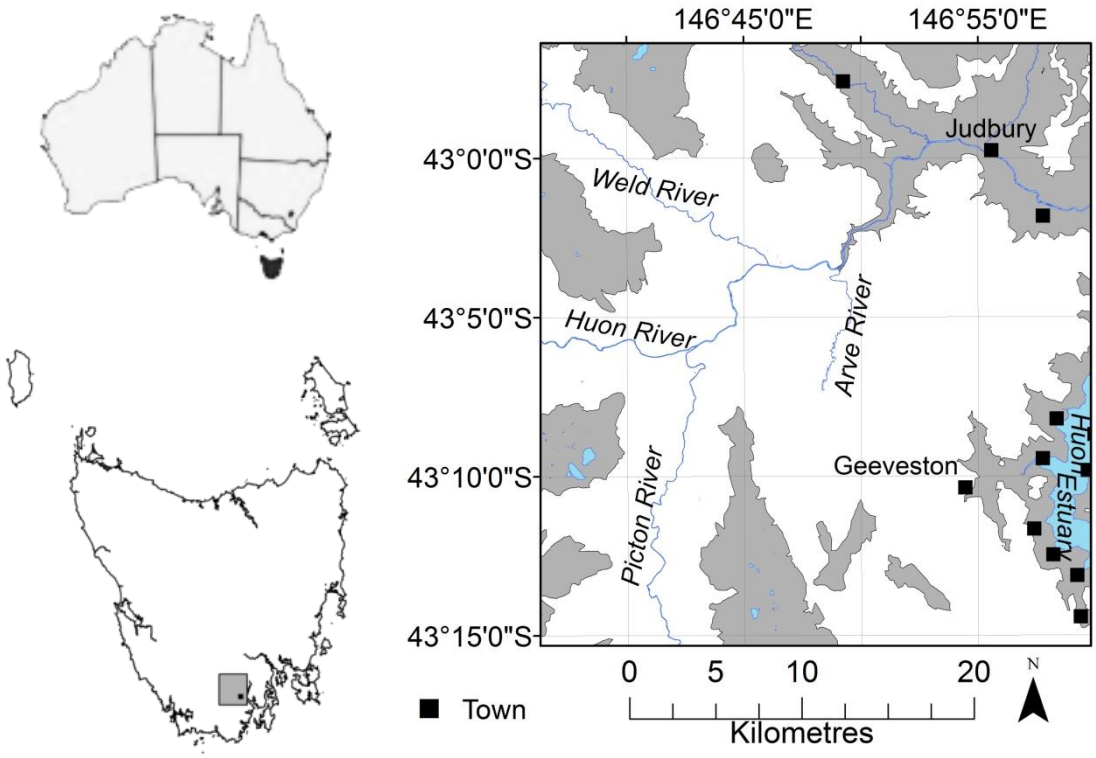

Figure 2-1. Map of study area.

State of Tasmania (Island) in Australia (top left) Tasmania showing location of the study region (bottom left); study area consisting of land below 600 m altitude with over 1000 mm annual rainfall in white (right). The names of two towns, Geeveston and Judbury, and the major rivers are identified to assist with spatial orientation.

The study area of 79,000 ha in Southern Forest Tasmania is below 600 m elevation and receives a mean annual rainfall of at least 1000 mm (Figure 2–1). Based on the interpolated climate data, BIOCLIM (Nix and Busby 1986), produced for Tasmania by Landscape Logic (2008), the study area means and standard deviations for minimum temperature (BIOCLIM parameter 6), maximum temperature (parameter 5), annual mean temperature (parameter 1) and annual rainfall (parameter 12) are estimated to be 1.3 ± 0.4°C, 19.7 ± 1.2°C, 9.5 ± 0.8°C and 1357 ± 213 mm, respectively. The four most common geological substrates are Jurassic dolerite, Permian mudstone, Triassic sandstone and Quaternary alluvium/talus (Laffan 2001). These produce a variety of soils capable of supporting both wet eucalypt forest dominated by *Eucalyptus obliqua* and/or *E. regnans* and cool temperate rainforest (Jackson 1968).

Settlement for agriculture began in 1836 and was concentrated near navigable waterways due to reliance on shipping for transport. Forest clearance was achieved by repeated vegetation 'burn-offs' after felling trees or ring barking them. Large areas of crown land were dedicated to state forest for timber harvesting in 1881 restricting further agricultural expansion.

Five major phases of forest exploitation have occurred in the study area: pining[6], splitting/pit-sawing[7], selective-logging[8], clear-felling[9] and plantation[10] (Kostoglou 1996). Huon pining and in-situ timber splitting and pit-sawing were phased out by 1880 or earlier. Impacts were confined to small patches and narrow riparian zones. Selective logging supplied mechanically powered mills from 1847. Harvesting rates were increased by the introduction of mechanical haulage systems after 1900, but impacts were also confined to areas within approximately 500 m of tramways, roads or mills. Slash residues were high following selective logging but from 1944, slash was burned (Forestry Commission 1945). Poor eucalypt regeneration at harvest sites prompted research in the late 1950s that culminated in the adoption of clear-fell silviculture (Cunningham 1960). This technique involves the felling of all or most trees within a site, referred to from here on as a coupe, which is then subjected to a high-intensity burn to reduce slash, expose mineral soil and create a nutrient rich ash bed. This procedure maximises eucalypt regeneration potential and reduces competition from rainforest and other tree species (Cunningham and Cremer 1965).

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[6] Pining is a term used to describe selective harvesting of trees in the Gymnospermae, commonly known as pines. In this region it refers particularly to the selective harvesting of *Lagarostrobos franklinii* (Huon pine) trees which were accessed along the river banks by boat prior to the development of road and tramways in the region.

[7] The earliest phase of harvesting native eucalypt timber involved sawing trees over pits or splitting the timber where the tree was felled. The sawn/split timber was then transported.

[8] Selective harvesting the selection of particular tree species and size classes for which a market demand existed, and resulted in many trees being left at the site. In most cases the target species were native eucalypts with small trees targeted for the production of fruit cases, and larger trees being targeted for furniture and floor board manufacture and other construction purposes. Particularly large trees, and those affected by rot were likely to have been left standing. This phase followed the development of tramway and road networks, which were required to transport whole logs to the local sawmills.

[9] Clearfell, burn and sow (CBS) operations target native eucalypt forest but result in the felling of all trees and understorey species. Following harvest, the site is treated with an intense burn and then aerially sown with seeds of native eucalypt species.

[10] The trees planted in this region are mainly exotic species such as *Pinus radiata* and *Eucalyptus nitens*.

Coupes are aerially sown with eucalypt seeds although in some cases retained seed trees provided a natural seed source. Clear-fell operations were first reported for the study area in the 1960/61 financial year. A local pulp mill commenced operations in 1963, providing a market for trees unsuitable for sawn timber production. Despite government promotion of timber plantations as early as 1920 only one had been established in the study area prior to 1985. Major plantation expansion occurred in the area from the early 1990s to compensate for reductions in forests available for wood production following expansions of the reserve network.

The removal of most of the remaining Aborigines from the region prior to 1836 resulted in the cessation of traditional Aboriginal fire management (Appendix 2.1.1). Wildfires in the study area after that time (Appendix 2.1.2) originated from a variety of anthropogenic sources: escaped camp-fires, vegetation burn-offs, clear-fell regeneration burns, and sparks from cigarettes, steam engines and other machinery (Forestry Commission annual reports). Lightning may have ignited some fires although historical climate records demonstrate lightening storms in Tasmania, until recently, have been associated with rain. In extreme weather (e.g. 1898, 1934 and 1967) fires spotting great distances reached the study area via the Weld and Huon River Valleys, driven by strong northwesterly winds. In such extreme weather conditions, some rainforest also burned.

In response to conservation concerns about the environmental impact of timber harvesting, the Forest Practices Code (FPC) was introduced in 1985 to regulate forest practices and was revised in 2000 (Forest Practices Board 2000). The FPC limits coupe size and aggregation while prohibiting harvesting in environmentally sensitive areas. In 1997 the Tasmanian Regional Forest Agreement (RFA) was signed between the State and Federal governments, reinforcing the FPC and protecting a substantial network of forest in both formal and informal reserves (Montreal Process Implementation Group for Australia and National Forest Inventory Steering Committee 2013). The environmental trade-off was the removal of annual harvest limits to facilitate a plantation-establishment program. This program was constrained by the Permanent Native Forest Estate Policy (PNFEP) that states that native forests will never cover less than 95% of their 1996 extent (Department of State Growth 2014). Revisions to the Permanent Forest Estate Policy also committed the

Government to have phased out broad scale clearing and conversion of forest on public land by 2010 and on private land by 2015 (Department of State Growth 2014).

2.4 Methods

Forest-type photographic interpretation (PI) mapping categories for the study area were reclassified using a rule set (Appendix 2.2) into twelve vegetation classes (Table 2–1) or water for the years 1947, 1985 and 2009. The vegetation classification was informed by disturbance history. Areas mapped as water in any year were erased from the vegetation maps of all years to reduce mapping discrepancies. Maps and disturbance data used for vegetation classification and spatial analyses are listed in Appendix 2.3, with additional metadata for PI maps provided in Appendix 2.4.

Following the general approach of Brown and Vivas (2005), each vegetation class was assigned a stability score between 0.5 and 10 (Table 2–1). The stability scores being estimates of the relative fire-free intervals required to maintain the vegetation, and prevent it converting into a different structural form. Hence, classes with higher stability scores are likely to have had less frequent, recent or severe disturbance, and are more likely to provide habitat for rainforest plants as well as other biota dependent on mature forest structures. Stability score maps were converted into 50 m pixel raster format, allocating each pixel the score of the predominant (by area) vegetation class overlaying it; no data values were applied to unmapped areas (water). LC was derived by calculating the mean stability score within the landscape surrounding each pixel; "no data pixels" (water and areas beyond the study area frame shown in Figure 2–1 were ignored. The landscape was defined as the area within a fixed radius of the pixel, the radius varying depending on the scale of analysis. Landscape areas with 500 m, 1000 m and 2000 m radius were each used to calculate LCI scores. LCI scores were rounded up when grouping into classes. Maps of LCI change between years were generated using a raster calculator to subtract LCI scores obtained in one year from another.

Only two data sources required digitizing: tramways and mills (1840–2009) and 1947 PI mapping. Figure four from Kostoglou (1995) and the 1947 PI maps covering the study area were scanned and saved as 300 dpi image files. The images were ortho-

rectified in ARCGIS. All tramways and mills mapped by Kostoglou (1995) were manually digitized together with those not appearing in Kostoglou's map but marked on the 1947 PI map. PI polygons from the original 1947 PI maps were hand traced onto acetate. The traced polygons were scanned (600 dpi) and image ortho-rectified and converted from raster to vector format automatically in *Landscape Mapper* (Myriax Software Pty Ltd 2008). Tagging (assigning PI-codes and associated data to each polygon) and final editing occurred in MAPINFO Professional version 9.5 (Pitney Bowes Pty Ltd 2008) and was exported to ARCGIS for classification and analysis.

Table 2-1. List of vegetation classes, definitions and stability scores (SS)

Code	Title/Definition	SS	Code	Title/Definition	SS
RAINF	*Rainforest*: Eucalypts <5 % cover, mapping indicates myrtles or other rainforest species (may include logged or recently burnt forest).	10	**SILVP**	Partially logged: Mature eucalypts >5% cover in forest logged or thinned in previous 50 years.	4
MIXED	*Mixed forest:* Eucalypts (mature or regrowth) >5% canopy density, myrtles or other rainforest species mapped (may include logged forest).	9	**SILOR**	*Older silvicultural regeneration*: Regrowth eucalypts >5% cover dominating over forest logged 20-50 years previously.	3
WFMAT	*Mature eucalypt forest:* Mature eucalypts >5% canopy, understorey not mapped as having rainforest species, no history of logging or clearance in recent 50 years but most likely to have been burnt in wildfires during previous 110 years.	7	**SILYR**	*Young silvicultural regeneration*: Regrowth eucalypts >5% cover in forest logged in previous 19 years.	2
WFRGO	*Older wildfire regrowth forest:* Regrowth eucalypts >5% cover, Mature eucalypts <5% cover, burnt and/or logged more than 50 years previously.	6	**NOFOR**	*Native non-forest*: Vegetation < 15 m tall, in which eucalypts provide <5% cover and rainforest species are not mapped (may include logged or recently burnt areas).	1
WFRGY	*Young wildfire regrowth forest:* Regrowth eucalypts >5% cover dominant; Mature eucalypts <5% cover; forest burnt in previous 50 years without a history of logging or clearance.	4	**PLNTN**	*Timber plantation*: Land cleared and planted with trees for wood production purposes.	0.5
OTHNF	*Other native forest*: Eucalypts <5% cover, no rainforest species mapped, dominant canopy trees >15 m tall (may include logged or recently burnt forest).	4	**AGRIC**	*Agriculture*: Land cleared for agricultural or urban uses.	0.5

ARCGIS version 10.1 software (ESRI 2011) was used for all spatial classifications, area calculations, raster statistics and sampling. The geographic projection used for all maps and analysis was the Map Grid of Australia 1994, zone 55.

Vegetation covers are reported for those parts of the landscape below 600 m and receiving more than 1000 mm rainfall in the study area (Figure 2–1). Mean and standard deviation of the LCI score by year for the study area and each component vegetation class were calculated, but only for parts of the study area that were 1 km or more inside the frame enclosing the study area. All pixels within landscapes extending beyond the study area but not beyond the rectangular frame were used in the calculation of LCI metric scores for all pixels within the study area.

The study area was partitioned into an eastern and western region, the regions being divided along a boundary representing the western limit to logging and roads in 1947 to determine whether LCI varied because of the two different types of disturbance history.

Random points were used to analyse LCI change through time and correlations between pixel stability score and LCI score for different spatial scales and years. Up to 30 randomly sampled points were generated for each vegetation class in 1947 and then divided into subgroups of logged or not after 1947. Point locations were constrained within each class so that they could not be closer than 500 m, limiting the number of possible points. In all 340 random points were generated.

Coupes logged during a ten-year period before the FPC was introduced (pre-FPC: 1975–1984), just after (post-FPC: 1986–1995), and following the RFA (post-RFA: 1999–2008) were selected for comparative analysis if they were entirely contained within the study area frame, did not extend beyond the study area boundary by more than 500 m and had more than 57% of their area within the study area.

The effect of differences in coupe area and configuration resulting from changes in government regulation between the three decades was tested first by assuming coupes within each period were uniformly occupied by young silvicultural regeneration (SILYR) and surrounded by mature eucalypt forest (WFMAT). From this artificially contrived vegetation pattern, one km radius LCI maps were prepared for each period

and LCI mean and standard deviation calculated for coupes logged in each decade. ANOVA was used to test differences between the decades and regression analysis was used to test correlation between factors and within each decade using software package Minitab 16.1.0 (Minitab Inc, 2010).

To determine the relative importance of coupe configuration compared with historical changes to landscape, vegetation maps were interpolated for the start of each decade using all available mapping and disturbance data. Vegetation maps for the end of each decade were also prepared, but, instead of interpolating vegetation on the basis of time since disturbance, all vegetation at the beginning of the decade was assumed to have remained unchanged, except if it had been logged or converted to plantation within that decade. In this way influences on LCI from wildfires or maturing vegetation were artificially removed from the analysis. Areas disturbed by logging or conversion to plantation were mapped to vegetation classes reflecting later PI map data. One km radius LCI maps were then prepared for the beginning and end of each decadal period. LCI change maps were then calculated for each period and classified into 0.1 LCI unit classes. For selected coupes, the mean distance to coupe edge, mean stability score and mean one km LCI score for the beginning of the period were then calculated for each LCI change class for each period. The relationship between each parameter and LCI change classes was investigated within and between periods using ANOVA.

2.5 Results

2.5.1 Changes in vegetation between 1947 and 2009

2.5.1.1 Stages in landscape fragmentation

In 1947 and 1985 the study area met the definition of an intact landscape (*sensu* McIntyre and Hobbs 1999) with more than 90 % native vegetation. However, even in 1947, more than 12% of the eastern subregion had been cleared for agricultural land uses (see Appendix 2.5) and already met the definition of a *variegated* landscape (*sensu* McIntyre and Hobbs 1999). By 1985 clearance for agriculture and plantation had increased in the eastern part of the study area but only about 100 ha of the

western area had been cleared. In 2009 the region as a whole met the definition of a *variegated* landscape, since more than 14 % had been deforested (Appendix 2.6). However, conversion to agricultural land and plantations still only affected 2% of the western subregion, while in the east clearance had reached 27%.

2.5.1.2 Vegetation

The greatest vegetation change between 1947 and 2009 was in the replacement of mature forests (particularly mixed forest) with silvicultural regrowth forest types (Figure 2-2). Mixed forest reduced by nearly two thirds (63%) of its initial area (Figure 2-2a). Mature eucalypt forest (WFMAT) declined by just over one third of its 1947 extent (35%). However, the amount of rainforest (RAINF) remained stable. About 21800 ha (~60%) of forest mapped into these three mature forest types in 1947 were no longer attributed to any of these classes in 2009. Of this forest nearly 14,250 ha had been logged, 2200 ha had been converted for plantation or agriculture and 3500 ha were burnt in wildfires after 1947. Remaining changes in classification could not be attributed to known causes and may be due to discrepancies in mapping or declines in mature eucalypt densities leading to reclassification into other classes (OTHNF, NOFOR or WFRGO).

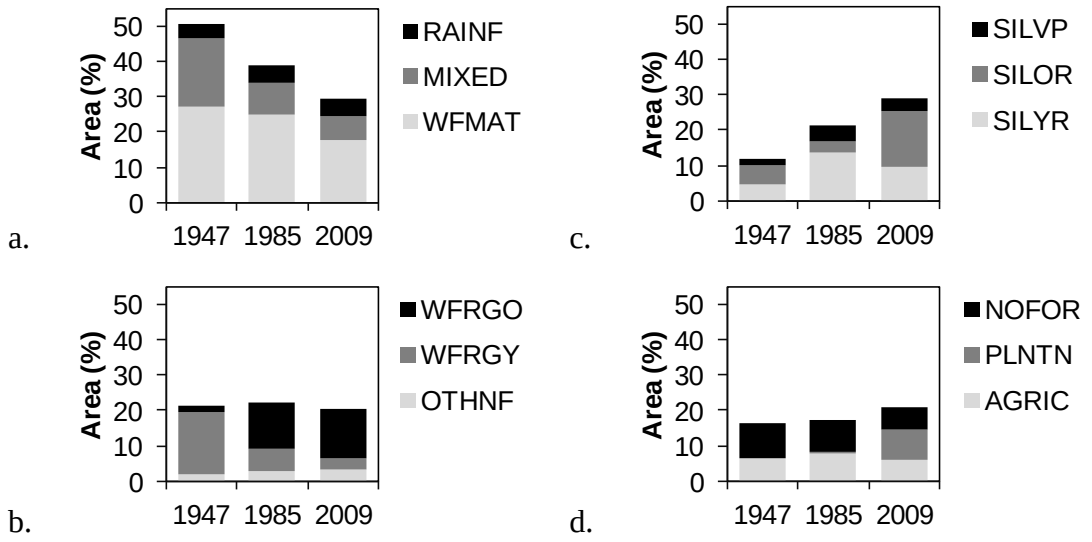


Figure 2-2. Percentage of the total study area (~72,600 ha) occupied by 12 vegetation classes in 1947m 1985 and 2009: a) mature forest types; b) wildfire regenerated regrowth forests; c) harvested regrowth forest; d) non-forest and cleared land; see Table 2–1 for explanation of vegetation codes.

At all three time periods nearly 20% of the study area was occupied by wildfire-generated regrowth eucalypt forests, which lacked mature eucalypts (WFRGY & WFRGO), but more than 90% of these forests were under 50 years old in 1947 whereas 82% had not been burnt for more than 50 years in 2009 (Figure 2–2 b).

The proportion of the study area occupied by forest in an early stage of succession due to timber harvesting (SILYR, SILOR, SILVP) increased from 10 to 27% between 1947 and 2009 (Figure 2–2c).

The area of cleared land (AGRIC and PLNTN) more than doubled between 1947 and 2009 (from 4500 ha to 10550 ha). Between 1985 and 2009 plantations (PLNTN) increased from 300 ha to 6300 ha of which only 1700 ha were established in areas previously cleared for agriculture. About 700 ha of plantation were established in areas mapped as non-forest in 1947. A large proportion of this area was likely to have been abandoned farmland, and partially explained the reduction in non-forest between 1947 and 2009. Likewise 1100 ha mapped as non-forest in 1947 were later cleared for agricultural use and may also have been either abandoned farmland or land affected by timber harvesting that had not regenerated back to forest at the time of mapping in 1947.

In 2009 the majority of the study area was still native forest (79%). However, only 21% of this remaining forest area had no documented history of disturbance from wildfire, logging or clearance. About 2% of forest had recolonized cleared land, 40% had been subject to timber harvesting and 37% had no documented history of logging but had been burnt by wildfire in the previous 110 years.

2.5.2 Observed patterns in landscape context

2.5.2.1 Overview of landscape context patterns

In all three years the region was strongly divided east-west into low and high LCI scores, a pattern that became more pronounced with increasing landscape size (Figure 2-3). The gradient in LCI across the study area was evident also in the frequency distribution of LCI classes between the two subregions (Figure 2-4b). Despite this contrast, there was only weak evidence that the frequency distribution of LCI change

scores measured in each region differed either for the 1947 to 1985 period (Figure 2-5b) or the more recent period (Figure 2-5c).

Mean LCI for the study area declined from 5.3 in 1947, to 4.3 in 2009 at all spatial scales (Figure 2-4a, Appendix 2.7). Considerably less of the study area had LCI scores above seven in 1985 and 2009 compared with 1947 (Figure 2-4a). All three years had similar areas of LCI scores below 2 but varied greatly in the frequency of LCI scores between 2 and 4.5 (greatest for 2009) and between 5.5 and 7 (greatest for 1985, Figure 2-4a).

The most extreme reductions in LCI score (a LCI change score of between -7 and -3), were more common between 1947 and 1985 but affected only a small proportion of the study area (Figure 2-5a). The western subregion had the greatest area of extreme reductions in LCI with 19% of its area having changing by between -7 and - 2.0 LCI units. A greater proportion of the study area was affected by negative changes in LCI score in the period 1985 to 2009 period than in the earlier period (Figure 2-5a, 65% of eastern subregion and 46% of the western subregion). Conversely, a much smaller proportion of the study area was observed to have a positive change in LCI score in the recent period, with the greatest concentration of the increased LCI scores occurring in the western subregion (Figure 2–5).

2.5.2.2 Landscape context within vegetation types

The mean LCI scores for most vegetation classes declined between 1947 and 1985 and between 1985 and 2009. This trend was consistent for both periods at all spatial scales for the three most mature forest classes (RAINF, MIXED, WFMAT) and older wildfire regrowth forest (WFRGO, Figure 2-6, Appendix 2.5, Appendix 2.7.

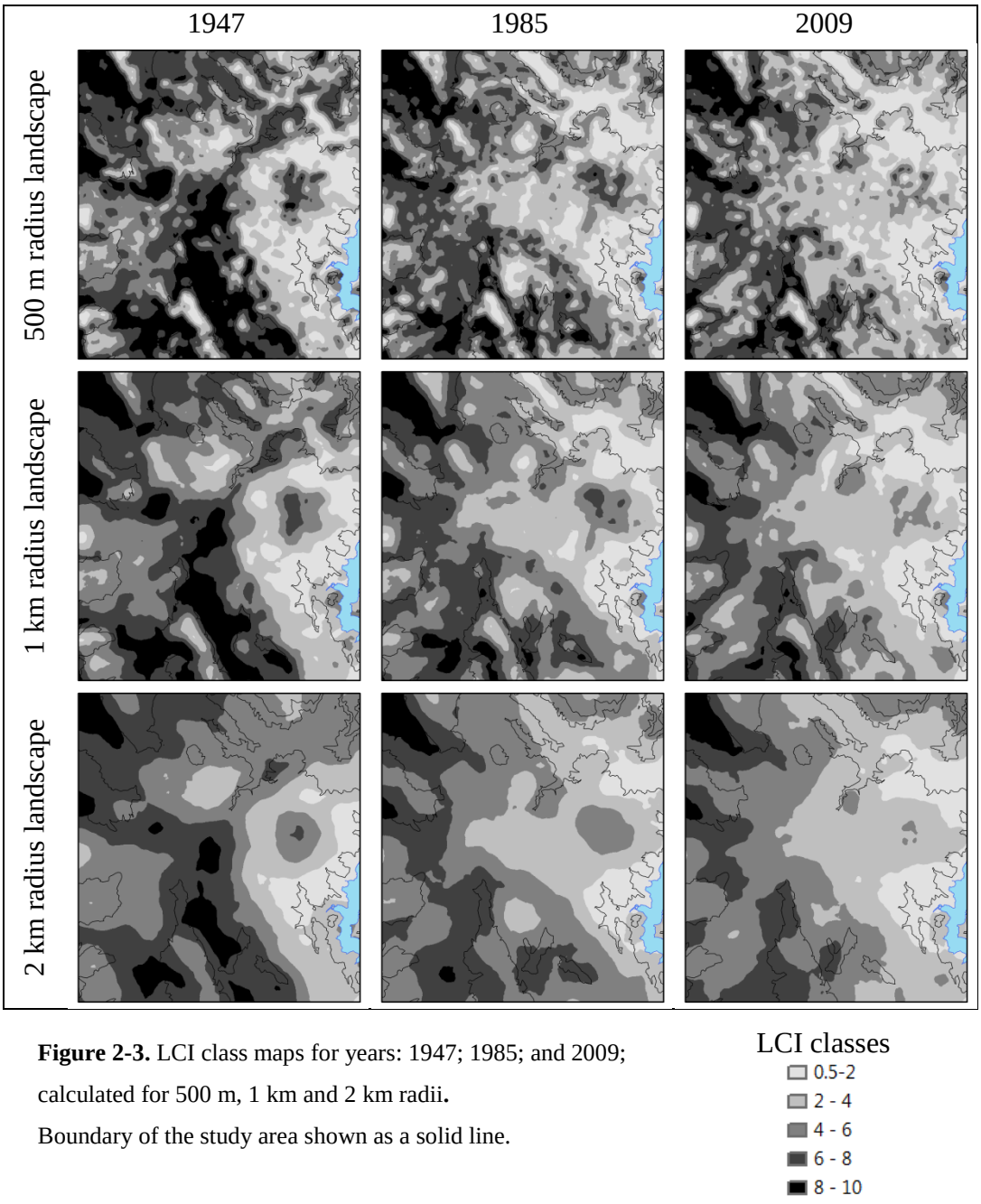


Figure 2-3. LCI class maps for years: 1947; 1985; and 2009; calculated for 500 m, 1 km and 2 km radii**.**
Boundary of the study area shown as a solid line.

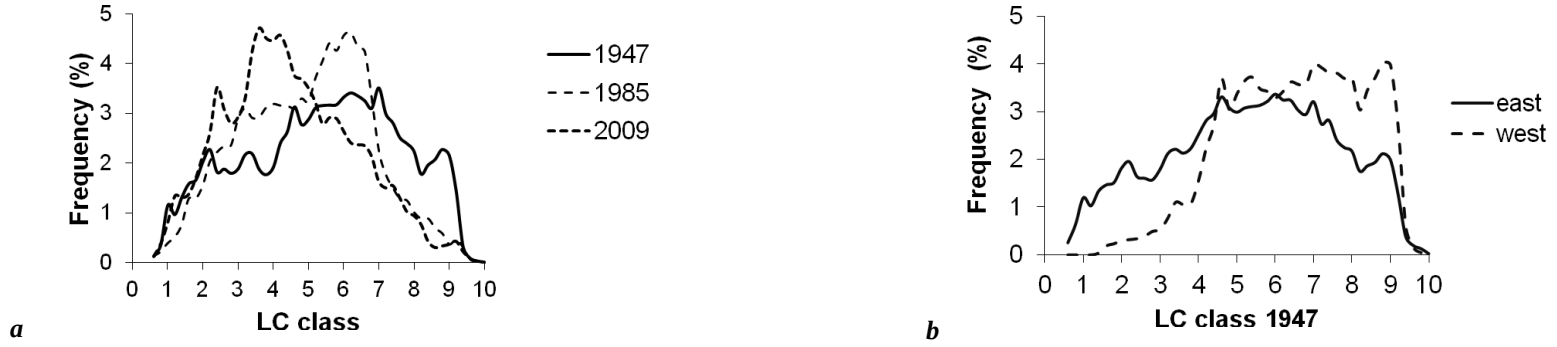


Figure 2-4. Frequency distribution of pixels in LCI classes (0.2 unit intervals, 1 km landscape radius) within a) the whole study area for three years 1947, 1985 and 2009 and b) east and west subregions in 1947.

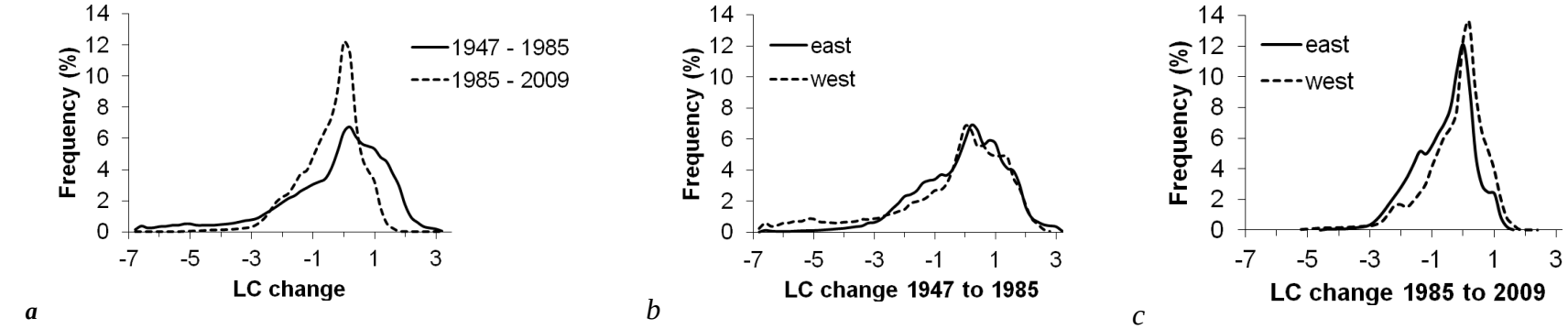


Figure 2-5. Frequency distribution of LCI change classes (0.2 unit intervals, 1 km landscape radius) within a) the whole study area for two time intervals, and for two subregions, for b) 1947 to 1985 c) 1985 to 2009.

The only vegetation class to show a consistent trend of increasing mean LCI score for both time periods and for all spatial scales was young silvicultural regrowth forest (SILYR, Figure 2-6, Appendix 2.7). The LCI scores in which these forests occurred ranged from 0.5 to 8.0 (Figure 2-6). In 1947 the frequency distribution for the 500 m and 1 km radius LCI scores for these forests were similar, with largest areas of this forest occurring in areas with LCI scores under 2 (Figure 2-6). In 1985 the frequency distribution peak in LCI scores was between 2 and 2.5 whereas in 2009 the majority of these forests occurred in areas with a LCI score over 3.0 (Figure 2-6).

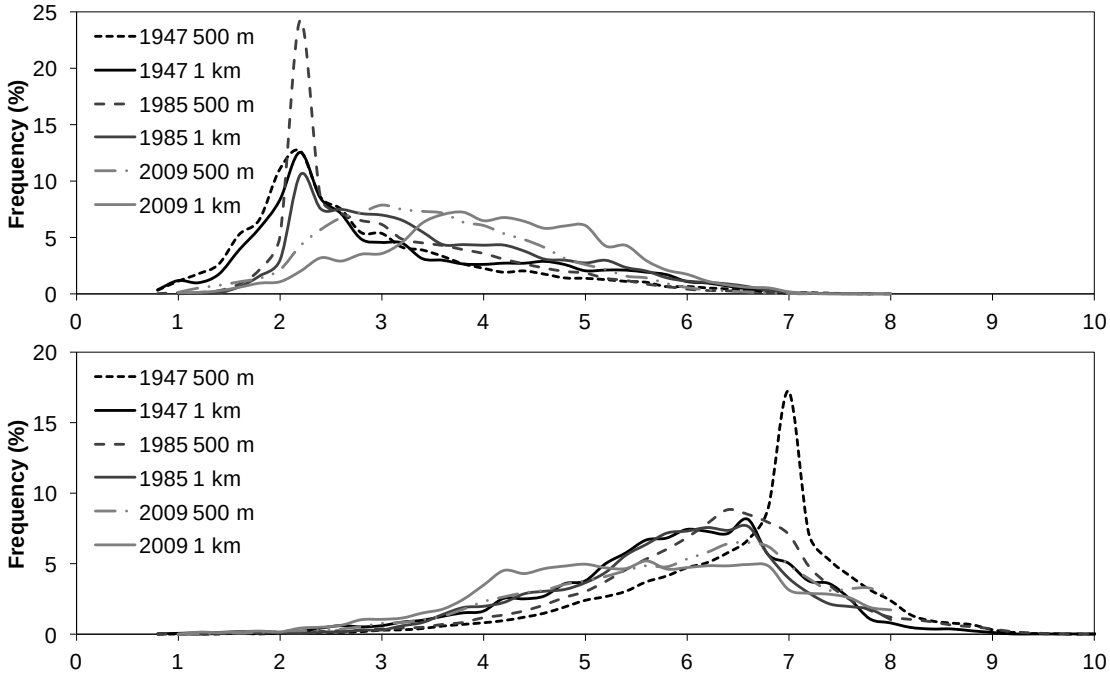


Figure 2-6. Frequency distribution of LCI classes (0.2 unit class intervals) by year and landscape radius within areas mapped as: above) young silvicultural regeneration (SILYR); and below) mature eucalypt forest (WFMAT).

2.5.2.3 Variability of landscape context within the study area, autocorrelation between LCI scales and patch size effects

There was strong evidence that the variance (i.e. standard deviation) and range of LCI scores in the 500 m radius around 340 random points reduced when the radius of the buffer window used to calculate LCI was increased from 500 m to 2 km (e.g. 1947 median std deviation of 500 m LCI score was 0.5 and 2 km LCI score = 0.18, Mann-Whitney w = 159621, $P < 0.0001$). The variance and range of the 2 km LCI score also

declined through time from 1947 through to 2009 (1947 median std deviation for 2 km LCI score = 0.18; 2009 median std deviation for 2 km LCI score = 0.14, Mann-Whitney w = 130862, $P < 0.0001$; see Figure 2-3, Appendix 2.7: Table 2-F). But the variance and range of 500 m LCI scores were greater in 2009 (median standard deviation 500 m LCI score = 0.55) than in 1947 (median standard deviation 500 m LCI score = 0.50) but the differences in variance were not sufficiently large to be distinguished from chance variation, and the evidence for a difference in the range of scores was weak (W = 110499, $P = 0.040$).

The observed spatial patterns in LCI were robust for different spatial scales demonstrating spatial autocorrelation. For example, in 2009 the LCI scores calculated at the 500 m radius explained 83% of variance in LCI scores calculated for the 1 km radius for 340 randomly located points. Similarly, in 1947 the 500 m LCI score explained 87% of variance in the 1 km radius LCI score.

LCI scores were also correlated between years. For example, the 1947 LCI scores calculated for 500 m radius explained 32% of the variance in LCI for the same scale in 1985 and 36% of that for 2009 for 340 randomly located points (data not shown). The 500 m radius LCI scores in 1985 explained 65% of the variance of 500 m radius LCI scores in 2009. Despite this the mean change recorded at these 340 random points was similar between 1947 and 1985 (-0.45 ± 0.12) to the change recorded between 1985 and 2009 (-0.53 ± 0.07). There was only a minor reduction in the correlation when comparing different years and different scales; for example the LCI scores in 1947 for the 500 m radius explained 44% of the variance in LCI scores in 2009 for the 2 km radius (data not shown).

Despite evidence that between 1947 and 2009 the 2 km LCI scores became less varied around 340 random points, the mean size of mapped vegetation classes declined over this time period and so did not explain the reduced variability. In 1947 study area 75% of the study area was occupied by patches of vegetation that were larger than 78.5 ha[11] while only five percent was occupied by patches under 7.8 ha. Hence, a large

[11] The 500 m radius landscape covers 78.5 ha.

proportion of pixels in 1947 had landscapes dominated by the vegetation patch within which the pixel was located. The spatial autocorrelation between pixel stability score and LCI score reduced with increasing landscape radius and time (Table 2–2). The explanation for the reduced variability was therefore not due to patch size but due to the greater proportion of the landscape occupied by vegetation at more similar or less

For the 1 km radius landscape (314 ha) 57% of the study area in 1947 was occupied by patches larger than the landscape radius, while for the 2 km radius landscape (1257 ha) 30% of the map was occupied by vegetation patches larger than the landscape radius. In 2009 only 52% of the study area had vegetation patches larger than the 500 m landscape radius, 27% for the 1 km radius, and less than 10% for the 2 km landscape.

Table 2-2. Variance (R^2) of the LCI score explained by pixel stability score in 1947 and 2009 and for three landscape scales

		Landscape Year	
		1947	2009
Scale	500 m	76%	64%
	1 km	60%	49%
	2 km	51%	40%

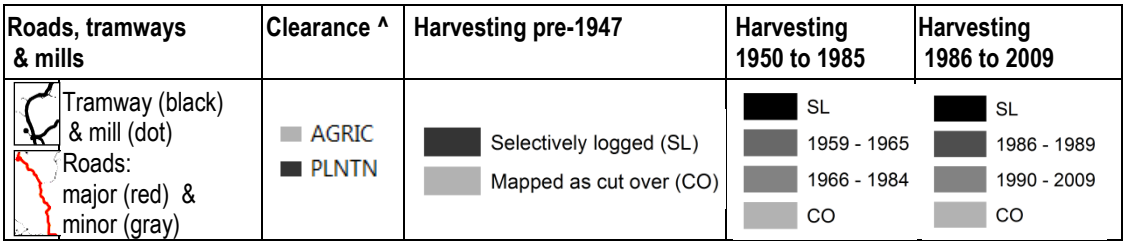
2.5.3 What were the drivers of landscape context change?

2.5.3.1 Overview

The differences in the LCI scores in the western areas in 1947 corresponded with patterns in wildfire distribution. The patterns of much lower LCI scores in the eastern part of the study area in 1947 corresponded with combined distribution patterns of cleared land, timber harvest areas and wildfire. Areas with landscape context scores of two or less (~ 10% of study area) in 2009 had already been heavily impacted by European disturbance before 1947. These areas had a mean 1 km radius landscape area of 50% logged or cleared before 1947 and were less severely affected by disturbance after 1947. LCI scores between two and less than four in 2009 had between 17% and 45% of their landscape cleared or logged by 1947 but had more than 45% of their landscapes affected by these disturbances after 1947. Areas with

LCI scores of between four and six in 2009 had less than 15% of their landscapes cleared or logged in 1947 but between 15% and 45% affected after 1947.

Figure 2-7. Disturbance history maps: 1947, 1985 and 2009 (see next page)



[#] Explanation for Wildfire classes used in Figure 2-7 legend:

'pole regrowth 1947' is a forest PI class most likely to have regenerated from wildfires in or after 1898 and before 1934;

'sapling regrowth in 1947' is a forest PI class most likely to have regenerated in wildfires between 1934 and 1947;

'fire damaged' (year) indicates area of PI mapping shown as fire damaged for which the actual fire year is not known but not long the year mapped.

[^] Explanation for Clearance classes used in Figure 2-7 legend:

AGRIC = agriculture or urban use;

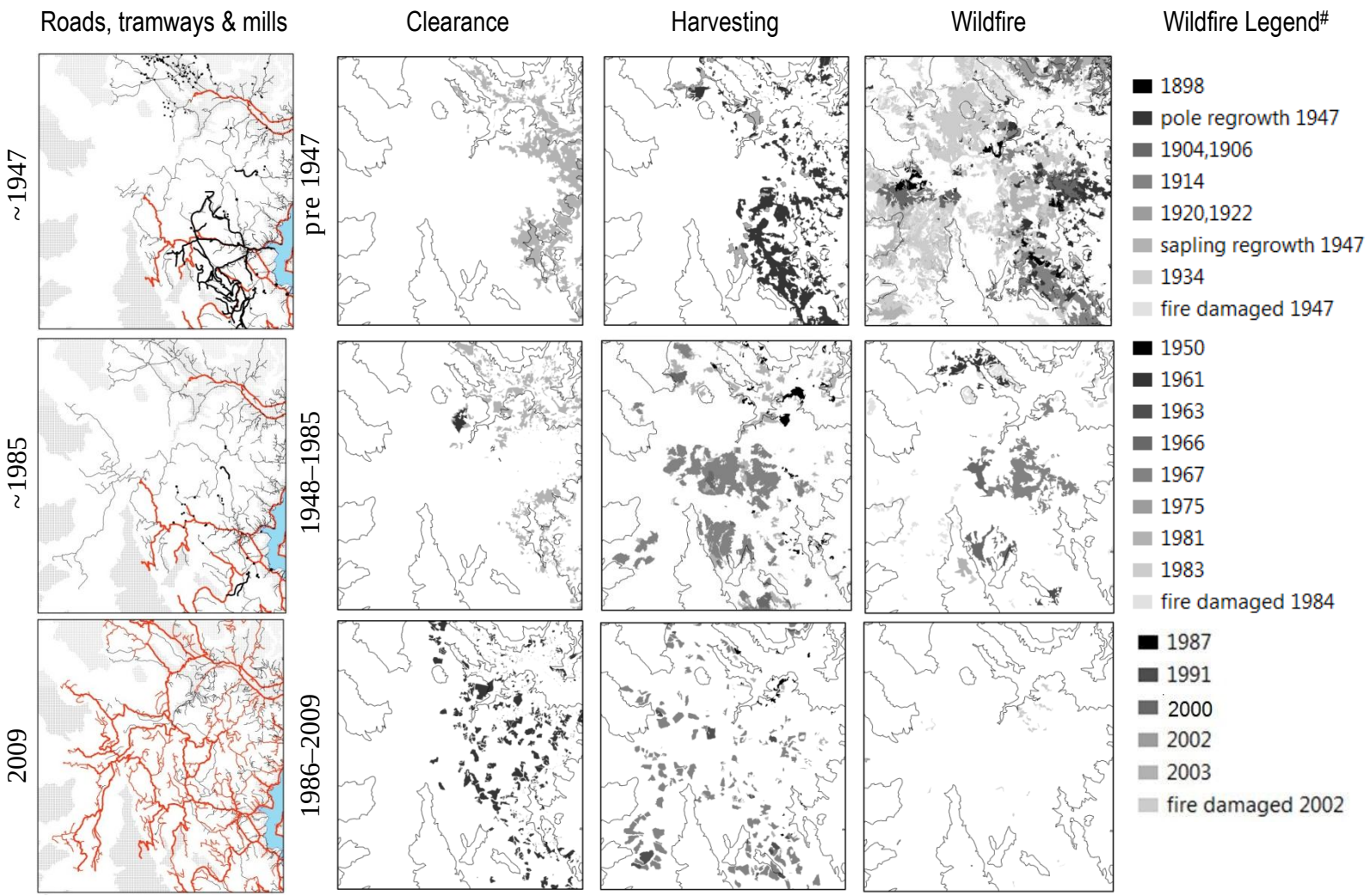
PLNTN = timber plantation.

Explanation of Harvesting codes used in Figure 2-7 legend:

Year range indicates when clear-felled forests were regenerated;

SL: Selectively logged, forest with >5% canopy density of regrowth eucalypt trees within 500 m of an operating tramway, road, mill or farmland was assumed to have been selectively logged;

CO: Mapped in PI map as 'cut over', indicating partial logging evident from imagery at the time of mapping.


Roads, tramways & mills
Clearance
Harvesting
Wildfire
Wildfire Legend#
~1947
pre 1947
~1985
1948–1985
2009
1986–2009
1898
pole regrowth 1947
1904,1906
1914
1920,1922
sapling regrowth 1947
1934
fire damaged 1947
1950
1961
1963
1966
1967
1975
1981
1983
fire damaged 1984
1987
1991
2000
2002
2003
fire damaged 2002

2.5.3.2 Clearance for agriculture

In 1947 agricultural settlement was aggregated in eastern parts of the study area in close proximity to the Huon estuary and major rivers. Areas mapped as agriculture correspond with the lowest scores in LCI maps for all three years (Figure 2-7). Despite increased road access, agricultural land expansion was largely confined to private land in eastern parts of the study area (Figure 2-7). About 3.4% of native vegetation was cleared between 1947 and 1985 for agriculture, a rate of 65 ha per year. Agricultural expansion including some that occurred in the drier areas beyond the study area led to an expansion of very low LCI classes in the northeastern edges of the study area. The clearance rate for agriculture reduced to about 22 ha per year after 1985 and contributed very little to changes in LCI score in the second period.

2.5.3.3 Clearance for plantation

Conversion to plantation was not confined to private land but government policy prevented the establishment of plantations adjacent to the World Heritage Area boundary, and so they remained concentrated in the east (Figure 2-7). About 4% of native vegetation was cleared between 1947 and 1985 while between the shorter period of 1985 to 2009 the clearance rate trebled from 77 ha per year to 234 ha per year, mostly for the establishment of timber plantations. A comparison of conversion rates for three decadal periods showed that no areas were converted to plantation in the decade pre-FPC, 67 ha per annum were converted in the decade post-FPC and 435 ha per annum were converted in the decade post-RFA. Forest conversion to plantations contributed substantially to the reduction in LCI score between 1985 and 2009 in eastern areas (Figure 2-8).

2.5.3.4 Wildfires

Landscape scale fires (>1500 ha) occurred in 1851, 1854, 1885/86, 1898, 1906, 1914, 1922, 1934, 1950/51 and 1966/67. Smaller fires were more frequent (Appendix 2.1.2: Table 2–A). Wildfires were not mapped within non-forest (e.g. farmland and montane and lowland moorland). Wildfire prior to 1947 affected a much greater proportion of

the study area than fires after 1947. In the 50 years prior to 1947 750 ha of forest per annum were burnt in wildfires compared with 195 ha of forest per annum between 1947 and 1985 and 16 ha per annum after 1985. Some areas burnt by wildfire during the 1960s were logged shortly after in timber salvaging operations.[12] Wildfires were not closely associated with proximity to roads and were not restricted to areas previously logged (Figure 2-7). Even taking into account unmapped areas of non-forest likely to have been burnt, there is no obvious relationship between the distribution of wildfires and the east-west gradient observed in LCI score maps for 1947 (Figure 2-3). Nevertheless, wildfires that occurred in the period 1947 to 1985 did contribute to the reduction in LCI scores, although the gradient was less steep than that associated with timber harvesting (Figure 2-8).

2.5.3.5 Timber harvesting

In 1947 timber harvesting in the preceding 50 years was estimated to have affected at least 9100 ha of forest and was aggregated along tramways, roads and in the vicinity of settled areas and sawmills (Figure 2-7). Areas of concentrated timber harvesting were associated with low LCI scores. The tendency for harvesting operations to be much more widely scattered throughout the region rather than aggregated on a frontier commenced in 1975 with the establishment of extensive new road access into western areas. This created greater heterogeneity in the LCI scores around these dispersed coupes in the 1985 and 2009 LCI maps. This was evident in the increasing pixilation in the LCI maps especially at the 500 m scale.

[12] The maps of wildfire affected areas intended to include areas subsequently logged, but mapped extents are almost certainly incomplete in salvage logged areas because the PI-maps provide harvest dates and are not explicit about preceding wildfires.

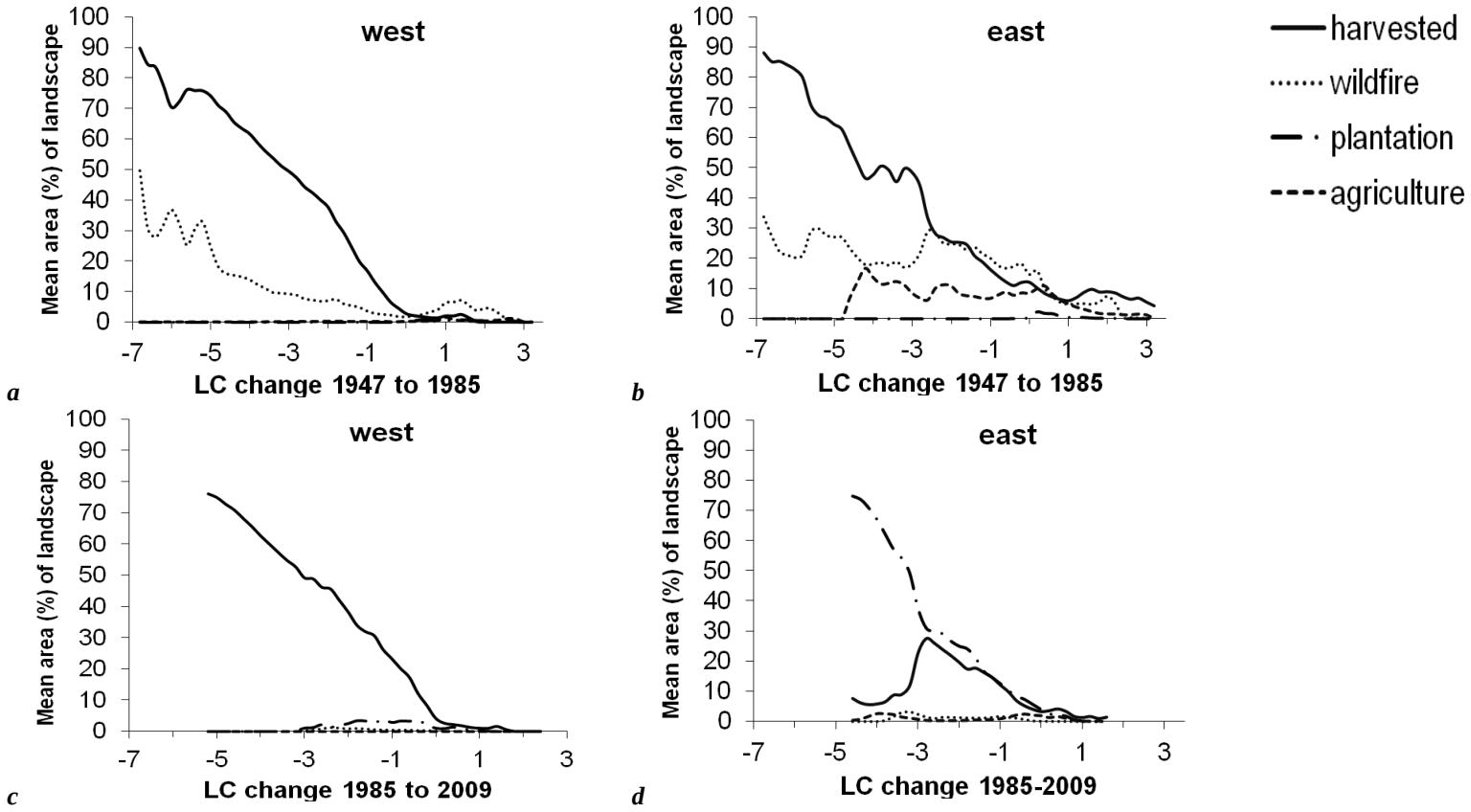


Figure 2-8. Mean proportion of landscape disturbed within each LCI change class (0.2 unit intervals, 1 km landscape radius) for (left) western and (right) eastern subregions and for each time period (top) 1947 to 1985, and (bottom) 1985 to 2009, by four disturbance types. Note that areas affected by wildfire and timber harvesting were not mutually exclusive.

The estimated areas of timber harvesting in this region prior to 1947 were about 180 ha per annum. This reduced to about 135 ha per annum between 1947 and 2009, with similar annual harvesting rates observed between the two periods when areas converted to plantation were excluded. Data from the analysis of three decadal periods show harvesting rates went from an average of 318 ha per year pre-FPC to 221 ha per year post-FPC, to 358 ha per year post-RFA.

In the western subregion all areas where the LCI score reduced had higher proportions of their landscapes affected by timber harvesting than by wildfire or clearance (Figure 2-8). Timber harvesting affected close to half or more of the landscapes in eastern areas where LCI scores reduced by more than 3.0 units between 1947 and 1985. However, in the following period it was plantations that occupied most of the landscapes of areas where LCI reduced by more than 3.0 units.

Randomly located points within all vegetation classes had significant reductions in LCI score following harvest (Appendix 2.7: Figure 2-B) whereas no significant change in LCI score between years was observed for points not subject to logging. The magnitude of LCI change depended on the vegetation class logged and whether logging took place before or after 1985 (Appendix 2.7: Figure 2–B). For points located in more mature forest types (WFMAT, MIXED) the difference in LCI scores were large but resulted in slightly higher mean LCI scores than points located in vegetation classes with lower initial stability scores. Points harvested after 1985 had higher LCI scores following logging than points located in the same vegetation type logged before 1985.

2.5.4 Effect of regulations on coupe size and landscape context

Coupe size reduced from a mean of 62 ha ± 48 ha pre-FPC, to 47 ± 36 ha post-FPC and 35 ha ± 29 ha post-RFA. The change between pre-FPC and post-RFA was unlikely to be due to chance variation (($F_{2,198}$ = 9.87; MSE = 1.27E11, $P < 0.001$). Coupes in the western areas were larger than those in the east in all decadal periods but the difference in mean size between the two areas only achieved significance ($F_{1,43}$=7.73, MSE=2.02E11, P=0.008) in the pre-FPC period (east = 40 ± 37 ha; west = 78 ± 49).

Despite the reduction in coupe size, scenario one models, which took into account coupe size and configuration but removed historical landscape variation, demonstrated no differences in the effect of harvesting practices (coupe size and aggregation) between the three decades on the average LCI scores within young silvicultural regeneration for the whole study area (Table 2–3). However, when eastern and western sections were considered separately, the effects of regulation and policy on mean LCI within silvicultural regeneration became significant. In the eastern section of the study area mean LCI of silvicultural regeneration declined significantly ($F_{1,73}$=5.13, MSE=0.403, P = 0.03) following the RFA compared with the Pre-FPC decade (Table 2–3). In the western section of the study area the mean LCI score in silvicultural regeneration increased significantly ($F_{2,102}$ = 8.1, MSE=0.31, *P* = 0.001) over the three decadal periods: Pre-FPC (5.3 ± 0.7), Post-FPC (5.7 ± 0.6), Post-RFA (5.9 ± 0.4).

Using the actual vegetation classes initially present in the landscapes but adopting scenario two in which these classes remained constant apart from changes resulting from logging and regeneration to native forest (SILYR) plantations (PLNTN) the mean LCI for the regenerated forest areas would have been 4.2 ± 1.2 in the pre-FPC decade, 4.6 ± 1.0 post FPC and 4.3 ± 1.0 post RFA (Table 2–3). The greatest LCI declines observed within these coupe areas were -5.3 pre-FPC, -5.4 post-FPC, and -3.2 post-RFA. There was strong evidence that the mean LCI scores for coupes in western areas were higher than those in eastern areas for all three decades ($F_{5,195}$ = 9.71, MSE = 0.921, *P* < 0.001). The higher mean LCI scores observed for coupes following a decade of harvesting in the western part of the study area post RFA compared pre-FPC was insufficient to reach an alpha level of significance. Mean LCI scores of coupes after a decade of harvesting in eastern areas also decreased following the introduction of the FPC in the eastern areas, increased marginally following the introduction of the RFA, but the differences in mean scores between these decades were also insufficient to distinguish from chance variation.

When the initial LCI scores were deducted from the final LCI scores there was evidence that the mean change in LCI score due to timber harvesting was different in eastern areas from western areas and between decades. For example the change in LCI scores was larger post-RFA compared with the change to LCI scores in logged

areas of eastern areas pre-FPC (F1,73=5.20, MSE=0.404, $P = 0.024$). In contrast there was a much smaller reduction in LCI scores in coupe areas post- RFA compared with pre-FPC in the western areas (F1,78 = 49.67, MSE=0.418, $P < 0.001$).

Table 2-3. Mean coupe 1 km LCI score (± standard deviation) before and after each decadal period for two modelling scenarios (n= number of coupes)

		Pre-FPC (1974–1984)		Post-FPC (1986–1995)		Post-RFA (1999–2008)	
Region	Scenario:	1	2	1	2	1	2
east	initial	n = 18 7.0 (± 0.0)	n = 18 4.5 (± 1.4)	n = 21 7.0 (± 0.0)	n = 21 4.9 (± 1.2)	n = 57 7.0 (± 0.0)	n = 57 5.1 (± 0.9)
	final	n = 18 6.0 (± 0.5)	n=18 3.8 (±1.3)	n = 21 5.6 (± 0.5)	n = 21 4.0 (± 1.0)	n = 57 5.6 (± 0.7)	n = 57 3.9 (± 0.9)
	mean change in coupe LCI score over decade		-0.8 (± 0.8)		-1.0 (± 0.4)		-1.2 (± 0.6)
west	initial	n = 27 7.0 (± 0.0)	n = 27 6.8 (± 0.9)	n = 25 7.0 (± 0.0)	n = 25 6.4 (± 1.3)	n = 53 7.0 (± 0.0)	n = 53 5.8 (± 0.9)
	final	n = 27 5.3 (± 0.7)a	n = 27 4.7 (± 0.9)	n=25 5.7 (± 0.6)	n=25 5.0 (±0.9)	n = 53 5.9 (± 0.4)	n = 53 4.8 (± 0.9)
	mean change in coupe LCI score over decade		-2.1 (± 1.0)		-1.4 (± 1.0)		-1.0 (±0.4)
whole	initial	7.0 (± 0)	6.3 (± 1.5)	7.0 (± 0)	6.6 (± 2.4) ^	7.0 (± 0.0)	5.5 (± 0.9)
	final	5.6 (± 0.7)	4.2 (± 1.2)	5.6 ± 0.6	4.6 (± 1.0)	5.7 (± 0.6)	4.3 (± 1.0)

Scenario 1 and 2 are described in methods.

^ The apparent discrepancy between LCI score mapped for coupes in 1985 compared with beginning of decade for post-FPC coupes (i.e. 1986) is due to changes in LCI scores associated with forest aging, in particular forests converting from 19 years old (SILVYR) in 1985 to 20 years old (SILVOLD) in 1986.

Distance to coupe edge was also positively associated with a reduction in mean LCI score. This relationship was strongest post-FPC ($R^2 = 0.72$), weak for pre-FPC ($R^2 = 0.44$) and poorly correlated in the post-RFA ($R^2 = 0.11$). The maximum average distance to coupe edge recorded for the LCI change classes was 309 m Pre-FPC, 571 m post-FPC and 180 m post-RFA.

LCI change classes were correlated with initial stability score (pre-FPC: R^2=0.94; post-FPC R^2=0.92, post-RFA: R^2=0.31). In the first two periods reductions of more than 3 LCI units were associated with average initial stability scores of more than

seven (pre-FPC: 7–9.0; post-FPC: 9–10). All observed LCI classes for the post-RFA period had an average initial stability score of less than 7.0.

Reductions in LCI score were positively correlated with mean initial LCI score (pre-FPC: R^2=0.94; post-FPC R^2=0.95, post-RFA R^2=0.64). In the post-RFA period the largest reduction in LCI score was -3.2 and was associated with an average initial LCI score of 5.8. Much higher initial LCI scores were present in earlier periods, the highest being recorded in the post-FPC decade, and were associated with much greater reductions in LCI score.

2.6 Discussion

2.6.1 Limitations and advantages of the LCI metric

The LCI metric used in this study successfully integrated the effect of several disturbance agencies and enabled these combined impacts to be visualised, illustrating landscape disturbance intensity across the study region. It was a simple and easy metric to generate and so may be a potentially useful tool for monitoring landscape change through time and space elsewhere. In contrast, McIntyre and Hobbs (1999) framework of landscape fragmentation is guided principally by the percentage of vegetation cleared. Their model has no quantitative means of taking disturbance effects on vegetation into account. It is also hampered by measuring change within specified areas, which, depending on the boundary, may hide more localised areas of fragmentation and degradation. According to their framework, the present study area did not reach the variegated threshold until after the second period, yet part of the region had reached this quantum prior to 1947, and large areas had already been impacted by logging and wildfires.

Most studies of fragmentation and landscape context effects use a binary approach to habitat such as forest/non forest or habitat/non-habitat (e.g. Smith et al. 2009). This enables the use of widespread and common metrics such as total habitat amount, length of edge, and mean patch size to be readily calculated for sample areas. Binary approaches to the description of quantification of landscapes may be of limited value for the modelling some fauna species leading to the development of alternative

landscape modelling approaches such as the variegated landscape approach (McIntyre and Barrett 1992) and the "continua-umwelt model" (Manning et al. 2004). Fischer and Lindenmayer (2006) proposed that important habitat gradients (food, shelter, space and climate) be explicitly included in landscape models for fauna. This approach is in keeping with a more functional definition of landscape connectivity that takes into account likely variation in species mortality and capacity for movement within the matrix (Villard and Metzger 2014; Tischendorf and Fahrig 2000a, b). The new LC metric described here, may provide a useful tool for landscape gradient modelling (*sensu* McGarigal and Cushman 2005), providing a means of visualising the degree of disturbance or vegetation maturity in the surrounding landscape.

It is not known yet, to what extent landscape context is an important driver of the presence and abundance for wet eucalypt forest biota. If it is an important, species are likely to respond in various ways to more than one attribute of landscape. It is known that disturbance frequency is an important driver of the presence and abundance of many plant and animal species within particular sites (Jackson 1968). Given this, it seems likely that a metric such as the one used here, which describes the surrounding vegetation in terms of its relative level of maturity or disturbance may be more useful than the commonly used patch metrics for modelling the landscape requirements of these species. The weighted averaging approach used to derive this particular metric could be applied to other mapped gradients such as climate, fertility (McGarigal et al. 2009).

Many studies have reviewed landscape metrics, describing, for example: their use; their many limitations and constraints; the difficulty of linking metrics unambiguously with the underlying mechanisms by which landscape may influence species responses which are likely to be complex, non-linear and interactive; and the problems they pose for analysis due to correlation with many variables; the sensitivity of analysis results to choices made in spatial resolution and landscape size (e.g. Tischendorf and Fahrig 2000a; Tischendorf and Fahrig 2000b; e.g. Li and Wu 2004; Cushman and McGarigal 2008; Cushman et al. 2008; Kindlmann and Burel 2008; McGarigal et al. 2009; Smith et al. 2009; Uuemaa et al. 2009; Peng et al. 2010; Wang and Cumming 2011; Kupfer 2012). The concerns that apply to landscape metrics generally will inevitably apply to this new metric. For example it is likely to be sensitive to variation in mapping

resolution, vegetation classification as well as the subjectivity and constraints of the scoring system applied in the calculation of the metric. In particular species distribution models that incorporate this LC metric will need to take into account the likely correlation between this and other LC metrics (Cushman et al. 2008), the patch stability score of the pixel as well as the autocorrelation between the same metric generated for different temporal and spatial scales. Despite these issues, the incorporation of this and metric in models may be acceptable, particularly where there are functional explanations for a species response to landscape variation (Smith et al. 2009).

The LC metric developed for this study was able to discriminate a trend of reduced maturity in the vegetation landscapes through much of the study area over time. It was also successful in discriminating differences in LC of coupes after logging that appeared to be associated with changes in policy and regulation. In contrast to the successful discrimination of differences in mean LCI scores in eastern and western areas and through time it was unable to discriminate differences in the LCI change in either of the two time periods examined for the east and west subregions despite very different disturbance patterns in the two regions and between two time periods. The apparent lack of sensitivity in the LCI change scores, may have been a perverse outcome due to the countering effects of increasing vegetation age with localised disturbance or else it may just be the failure of the LCI scores to reduce greatly in response to harvesting where LCI scores were already initially low due to historical disturbance in the eastern areas compared with the higher initial LCI scores in western areas.

Maintaining landscape heterogeneity has been recommended to land managers as a means of assisting in the conservation of biodiversity, particularly in regions where the matrix forms a significant ecological role in the maintenance of communities and populations (Chapter 14 in Lindenmayer and Fischer 2006; Lindenmayer et al. 2006). Landscape heterogeneity is usually considered distinct from the concept of the vertical structural complexity that is present within the locality of a patch. Landscape heterogeneity is usually defined in terms of the number of different types of patches or by the presence of marked environmental gradients in the landscape (Li and Reynolds 1994; Lindenmayer and Fischer 2006). This study did not investigate the

spatial patterns of either the structural vegetation complexity or the number and juxtaposition of vegetation types although it did document the change in the proportion of each mapped vegetation class present for each mapping year. Nevertheless, the LC metric used here did allow an indirect measure of spatial heterogeneity in the landscape, through the analysis of the variability and range of LCI scores present in the study area in each mapping year. Areas where the range of LCI scores were large and the variance of these high, are those that are likely to comprise of more varied vegetation types, with stronger contrasts in the maturity of different patches of vegetation. The analysis of the variance and range of LCI scores provided some evidence that this study area had become more homogeneous in 2009 compared with 1947 when it was LCI score was calculated using a 2 km radius. However, the scale at which the LCI score was calculated affected the outcome of this analysis with contrary trends observed between the results for the 2 km radius scores and the results using LCI scores calculated with a 500 m radius landscape buffer. This contrast is likely to be a response in the sensitivity of the scoring system to differences in the scale of vegetation heterogeneity, but demonstrated that a more direct measure of vegetation heterogeneity may prove simpler to interpret. Because the LCI metric used a weighted average system in its calculation, it was not possible to determine which combination of vegetation classes gave rise to particular scores. For examples a landscape with an equal mix of two very different vegetation communities such as rainforest and native non-forest receives the same LCI metric score (LCI = 5.5) as a landscape divided equally between mature eucalypt forest and partially logged mature forest, despite these forest communities being structurally and floristically quite similar. Despite this flaw, it is likely that in most real, rather than hypothetical situations, the weighting system does provide a score generally in keeping with the capacity of the surrounding areas to support mature forest species, the purpose for which it was designed.

Another consideration in using the metric is that the ratio between buffer size and patch size will determine the relative influence of the patch stability score on LCI score. If median patch size exceeds the buffer area then LCI score may differ very little from the patch stability score. While choice of buffer radius must take into account the effect of the original scale of mapping on patch-size and other aspects of

landscape heterogeneity (Meentemeyer and Box 1987), it should also reflect the scale at which the biota of interest respond to their environment (With and Crist 1995). That said, the strong correlation between LCI at different spatial and temporal scales means that it will be difficult to discern the specific temporal and spatial scale driving any observed associations between biodiversity and LCI score.

All metrics are inherently limited in their capacity to describe the aspects of landscape configuration relevant to biotic responses (Kindlmann and Burel 2008). More research is needed to know at what scale and which attributes of the landscape biota respond to landscape in wet eucalypt forest and whether the scoring system used to calculate the LCI metric reflects biotic responses in this forest system.

2.6.2 Social and government influence on variation between regions in levels of deforestation and fragmentation

Deforestation and associated landscape fragmentation is a major cause of global biodiversity crisis (Brooks et al. 2002; Boakes et al. 2010; Myers 1996; Laurance 2007; Glanznig 1995). In developed countries this process may be substantially influenced by pressure from local and global communities as well Government policy and regulation (Commonwealth of Australia 1995; Dargavel 1995; Shindler et al. 2002; Lindenmayer et al. 2004; Kingsford et al. 2009). The frontier region[13] studied here differs from many of the regions for which changes in LC patterns have been documented for Australia and overseas (e.g. see five representative examples cited by Lindenmayer and Fischer 2006). Many of the studies of landscape evolution involved a high conversion rate to agricultural land and plantation, which resulted in increased edge to patch ratios in which the remnant habitat patches became progressively more isolated within a matrix of agricultural and urban. The study area described here is distinguished by the high retention rate of native forest. Despite a more than 150 years or settlement and timber harvesting, 86% of the area remains native vegetation. Similar forest retention rates have also been observed in other production forest

[13] Frontier region is defined here to mean an area of intact native vegetation (in this case mainly forest) bounded on its edge by a settled area.

regions of the world (e.g. parts of the Pacific Northwest). Disturbance rates have often been associated with land tenure and can lead to strongly polarised landscapes (e.g. Spies et al. 2007). Within the study area private land tenures were restricted to the eastern areas and were associated with high rates of conversion to agriculture. In areas west of the study area the land was dedicated state reserve for nature conservation purposes, albeit mainly comprising either native non-forest vegetation or forests at elevations above 600 m. This distribution of tenures was spatially associated with the variation in LCI scores, a pattern which was exhibited at all spatial and temporal scales examined.

In Australia policies governing the release of crown land for alienation have resulted in regional variation in landscape fragmentation (Thackway and Lesslie 2009, Michaels et al. 2010). Government policies of the nineteenth century focused primarily on promoting the agricultural industry, leaving a legacy of remnant forest landscapes in matrix of agricultural land, examples of which include Tasmania's northern Midlands bioregion (Fensham and Kirkpatrick 1989; Michaels et al. 2010), parts of the northwest and King Island (Woolley and Kirkpatrick 1999), landscapes common throughout the Old World and now rapidly developing in the Amazon (Boakes et al. 2010; Laurance 2007) and central Africa (Bogaert et al. 2008).

Late in the nineteenth century, financial investments in the timber industry led government to dedicate substantial forest land to State forest, protecting it from agricultural deforestation. This tenure did not prevent forest conversion to plantation. Substantial areas of Tasmania's State forest have been converted to plantation, most recently following the RFA in 1997. It was only after government subsidies were provided for plantation establishment that the study region passed the threshold from being *intact* to a *variegated* landscape (*sensu* McIntyre and Hobbs 1999). Market-driven demand for environmentally certified timber products precipitated an end to the plantation expansion program in Tasmania before government limits were reached, a social factor affecting the timber industry in many countries, including Finland (Cashore et al. 2007). This social pressure resulted in recent government policy changes that prevent this region of Tasmania's Southern Forests from becoming *fragmented* (*sensu* McIntyre and Hobs 1999).

2.6.3 The effect of disturbance on landscape context

Consistent with other studies such as Broadbent et al. (2008) and Shearman et al. (2012), this study has demonstrated that the timber industry has been responsible for substantial shifts in disturbance regimes, leading to what Broadbent et al. (2008) term 'soft-edge' fragmentation, which is reported here as a reduction in LCI score in the study region since 1947. In 2009 only 21% of remaining forest had not been cleared, logged or burnt in the preceding 110 years, reflecting a significant shift in disturbance regimes since European invasion in the early nineteenth century. In contrast, about two-thirds of tall wet-forests in the adjacent Tasmanian Wilderness World Heritage Area are mapped without a regrowth eucalypt component, consistent with not having been burnt during the last century (unpublished data of author). The changes in stand age and LC patterns observed in the Pacific Northwest over a similar time period have were also associated with changes in disturbance regime associated with the timber industry (Hessburg et al. 2000; Hessburg and Agee 2003; Spies et al. 2007). Spies et al. (2007) was able to predict differences in several measures of both LC, forest structure and biodiversity when they simulated the effect of applying forest management policies in the Pacific Northwest through time. Several reviews of the ecological literature have clearly demonstrated that changes in LC metrics maybe correlated both with each other but also with various measures of biodiversity and ecosystem services (Spies et al. 2007; Broadbent et al. 2008; Turner et al. 2013). Broadbent et al. (2008) demonstrated how the expansion of timber harvesting results in a rapid increase in both a reduction in distance to edge and core to edge ratio. This in turn has been associated in some areas with the reduction in the prevalence of late succession species and an increasing abundance of species favoured by disturbance (Spies et al. 2007; Broadbent et al. 2008) The fact that vegetation can be substantially altered before significant deforestation has occurred (Broadbent et al. 2008) means it is insufficient to assess biodiversity impacts from landscape fragmentation on the basis of native vegetation extent data alone, at least for intact and variegated landscapes (McIntyre and Hobbs 1999; Thackway and Lesslie 2008).

2.6.4 How has policy, regulation and forest management practice influenced the landscape?

The largest reductions in LCI score between 1947 and 1985 were associated with timber harvesting, and since that time timber harvesting was also associated with the greatest reductions in LCI score in western areas. Between 1985 and 2009 in the eastern areas conversion of forests to plantations following harvest as well as harvesting contributed substantially to LCI score reductions (Figure 2–5).

In 1947 settled areas in the east of the region had much lower LCI scores than western areas which had been subjected only to wildfires (Figure 2-4). By that time, the area logged was already more than twice that of deforestation. After 1947 logging caused greater reductions in LCI score then either wildfire or deforestation in the region as a whole because it affected a much greater area (Figure 2-7). Land clearance for agriculture after 1947 was minor and limited to private land in the east that had usually already been logged and/or burnt. Plantations were at least partially located in areas previously cleared or logged, mitigating their contribution to reduced LCI scores. Nevertheless, they still contributed substantially to reductions in LCI score in eastern areas, particularly after 1996. After 1947, only one landscape-scale fire was mapped in the study area (Figure 2-7), but much of the area affected by this event had either been logged just prior to it, or was subsequently salvage logged in the following decade, confounding the effect of these different disturbance types.

Logging has been a major facilitator of deforestation in places like the Brazilian Amazon and New Guinea (Broadbent et al. 2008; Shearman et al. 2012). Kostoglou (1996) noted that, within the present study area, the establishment of saw-mills (to supply global timber markets in the nineteenth century) created nodes around which unplanned townships grew and agricultural development advanced. In contrast, a number of government surveyed townships failed to establish where no sawmills were developed. Logging offset or reduced the cost of converting forest for agriculture, but was certainly by no means a pre-requisite for deforestation. Critically in Tasmania, the gazetting of forest areas as State Forest land, was important in limiting the extent to which forests were cleared in Tasmania.

Due to the lack of available mapping and survey data the present study was not able to document pre-settlement to early settlement phases in the landscape evolution of the region. But for the period covered, unsurprisingly, there was a spatial advance of logging disturbance along transport networks from settled edges into forest landscapes, leading to major changes in LC well in advance of deforestation (Figure 2-7). This advance was by no means linear or uniform. It is evident that, from 1975, clear-felling operations leap-frogged substantial forest areas to harvest areas at the remote ends of road penetration before progressing back toward the settled regions. Clear-fell silvicultural systems adopting this harvesting pattern (also known as staggered-setting or checker-board) are common around the globe (Franklin and Forman 1987). This strategy may have occurred in earlier times, but, as all accessible and commercially valuable forest had been harvested by 1950 (Forestry Annual Report 1950/51), and the year of logging only mapped for clear-fell operations after 1963, it is not possible to provide supporting evidence. This harvesting method and pattern enabled the most valuable forests to be accessed, successfully regenerated and for the slash to be disposed of (Franklin and Forman 1987). Whether intentionally or not, it reduced remoteness of large areas of the forest estate, which in the social context of growing global pressure to conserve old growth and wilderness, reduced its value for reservation. Certainly, in recent negotiations towards a forest peace deal, environmentalists preferentially sought reserves in areas remaining unaffected by previous logging. Government provision of road infrastructure explicitly for timber harvesting purposes, made this leap-frog approach to harvesting economically feasible for industry. Whatever the motive, the effect of discontinuous harvesting did serve to reduce the concentration of logging from 1975. Prior to this time, harvesting, especially salvage-logging, occurred in aggregated areas contributing substantially to the larger reductions in LCI score observed between 1947 and 1985 in harvest areas (Figure 2-5).

In the nineteenth century timber harvesting was impeded in its expansion and characteristics largely by economics and technology. More recently industrial practices have altered in response to government regulation and market pressure to reduce the environmental impacts of harvesting. While a more detailed analysis is warranted, the data show government regulations from 1985 did result in logging

coupes becoming smaller and more dispersed. In western areas where plantations where timber production was not intensified by clearance for plantations, this policy also resulted in mean LCI scores being higher in coupes following harvest in the decades following the introduction of the FPC. Ecological theory (Baker et al. 2013b) suggests that the consequence of these policy changes at least in the western areas of the study area is likely to have been a reduced impact on biodiversity from logging at the harvest site compared to the impacts of earlier harvesting practices.

The shorter distances to coupe edges were associated with smaller reductions in mean LCI score for small coupes after harvesting compared with the longer distances to coupe edges in large coupes. Although the LCI metric was capable of demonstrating that modifying coupe size led to differences in LCI score following harvest, LCI scores following harvest were actually more sensitive to the stability score of the vegetation surrounding coupes and pre-harvest vegetation. Coupes in areas previously logged, or adjacent to plantations, farmland or early seral-stage forest, have lower LCI scores prior to logging and therefore harvesting resulted in smaller reductions in LCI score compared to harvesting in areas surrounded by mature forest. Therefore, in addition to changes in coupe size and configuration, historical declines in LCI were at least partially responsible for some of the observed reductions in the magnitude of LCI change after government regulation. Nevertheless, higher mean LCI scores for coupes after logging post FPC compared with pre-FPC (Table 2–3), particularly in western areas, and for scenario one modelling (in which vegetation differences were excluded) provided evidence that regulations were responsible for reducing declines in LCI score due to harvesting.

2.6.5 Implications for landscape resilience and biodiversity

The resilience of a landscape is defined here to mean the capacity for the landscape to influence recovery of biodiversity after perturbation back to its pre-disturbance state (Holling 1973). Hence the biodiversity will recover more quickly after disturbance in a patch within a more resilient landscape compared with a similar patch in a less resilient landscape. Clearly there are characteristics of the patch which will enable biodiversity to recover more or less quickly, but for this discussion it is the

characteristics of the landscape that enable them to influence biodiversity that is of greater interest here.

Numerous ecological studies have demonstrated associations between landscape composition and the capacity of forest patches to maintain diversity particularly of species dependent on late stage forest habitats (Forman and Moore 1992; Laurance et al. 1998b; Mesquita et al. 1999; Laurance et al. 2000; Lindenmayer and Fischer 2006; Baker et al. 2013b; Farmilo et al. 2014). In the area studied here there was evidence of changing landscape composition in the results which determined that there had been a reduction through time in the mean, range and heterogeneity of LCI scores. Both the empirical and simulation literature describing landscape ecology provides a foundation for the hypothesis that the observed changes in landscape composition within the study area may be associated with changes in recruitment and mortality rates for at least some species. Evidence from previously published studies within the forests of this study area have already demonstrated that distance to the nearest mature forest edge has an influence on the recruitment rates of several rainforest tree species (Tabor et al. 2007) and the recovery rate of beetle communities (Fountain-Jones et al. 2015). The mechanisms by which proximity to mature forest can facilitate recovery of mature forest species have been described in detail by Baker et al. (2013b).

The LCI metric provides a measure of the relative abundance of mature forest species habitats in the surrounding landscape of a site. Although not a direct measure of proximity, the more abundant mature forest habitat is then the closer it is likely to be. Biota (especially mature forest biota) in sites with higher LCI scores are likely to recover faster following disturbance compared with sites with lower LCI scores, all else being equal. The reduction in LCI scores and reduced abundance of oldgrowth forests observed in the study area since 1947 is therefore likely to have increased distances to the nearest mature forest and particularly an increased distance to oldgrowth forests. This is likely to have resulted in some loss of landscape resilience in many parts of the study area, but particularly eastern areas where agricultural land and plantations are concentrated. Although the response of biota to landscape is known to vary depending on scale and other aspects of the landscape composition, the observed correlations between LCI scores at different scales suggest that changes in

the LCI metric at any scale will give some measure of landscape resilience. Should wildfire occur now the recovery of at least some mature forest species may be slower than if LCI scores were higher and old growth forests formed a greater portion of the region.

Previous studies have also demonstrated that the direct effects of settlement, agriculture and logging also interact with and affect disturbance, including pollution, pest, weed and disease invasion on forest frontiers (Hobbs and Saunders 1994; McIntyre and Hobbs 1999; Saunders et al. 1999). In particular, fire regime change is common to many frontiers and has serious ramifications for biodiversity (McIntyre and Hobbs 1999; Shearman et al. 2012; Spies et al. 2012; Taylor et al. 2014). Small and landscape-scale fires were numerous in this region following settlement until the last recorded landscape-scale fire in 1967, observations which accord with those of Alcorn et al. (2001), Hickey et al. (1999) and Podger et al. (1988) for adjacent and overlapping regions. The limited available evidence suggests that fire was less frequent in wet forest and rainforest, at least for this area, prior to European settlement (Podger et al. 1988, Alcorn *et al.* 2001). More compelling evidence for vegetation shifts caused by both reduced and increased fire frequencies are provided for other parts of Tasmania (Podger et al. 1988; Ellis and Thomas 1988; Marsden-Smedley 1998; di Folco and Kirkpatrick 2013).

Fire extent and frequency after 1967 were much less than in the earlier post-settlement period. This is explained at least partially by increased awareness and regulation of ignition sources during high fire danger weather and improved fire suppression capacity. The reduction of slash by high intensity burning after clear-felling may also have reduced available fuel loads within youngest silvicultural forests compared with selectively logged areas. Since 1947 there has been a significant shift in demographic structure towards younger and more even-aged forest due to logging. Younger forests are more flammable than mature forests (Jackson 1968) and it is possible that higher densities of eucalypts in silvicultural regeneration create a more flammable forest-type than equivalent aged multi-cohort forest regenerated by wildfire. Shifts in the demographics of forest in the northwest pacific and southeast USA have resulted in increased continuity of fuel loads, increasing the probability of landscape scale and stand-replacing fires (Covington and Moore 1994a;

Hessburg et al. 2000). Taylor et al. (2014) detected a difference in the severity of fires burning in *Eucalypt regnans* forest depending on the age of the silvicultural regeneration, providing evidence that the most severe fires were associated with forests aged between seven and 36 years.

Although the results of the present study suggest the study area may be less resilient now compared with 1947, this is not surprising given that most of it is dedicated for timber production. The results also suggested that despite ongoing exploitation, government regulation in recent decades has contributed to the mitigation of LCI score reductions in coupes following logging in western areas of the study area. By dispersing coupes more widely and reducing their size, the LCI scores following harvest are now higher following logging compared with previous practices and it is likely that the mature forest biodiversity which is likely to be sensitive to disturbance, may have the potential to recover more quickly. Field survey work is required to test this hypothesis and to determine the nature of any relationship that may exist between native species and LC influence within the wet forest of this study area.

"... the first law of geography: everything is related to everything else, but near things are more related than distant things."

Waldo Tobler (1970) A computer movie simulating urban growth in the Detroit region. *Economic Geography*, 46(2): 234–240.

Chapter 3 Floristic response in silvicultural forest to distance from the mature forest edge

3.1 Abstract

This chapter tested the hypothesis that proximity to mature forest has an influence on the floristic composition of regrowth wet eucalypt forest in Tasmania's Southern Forests. To test this hypothesis five replicate sites from each of regrowth forest age classes (4-8; 23-28, 42-47 years since clearfelled) were surveyed (a total of 15 clearfell sites). Within each site three parallel transects were placed perpendicular to the boundary of an adjacent mature forest patch and quadrats (10 x 10 m) were located at seven distances (-35, -15, 15, 35, 70, 120 and 200 m) from the mature forest edge.

The data demonstrated there were large differences in the floristic composition of silvicultural forest from the adjacent mature forest, and that the silvicultural regrowth forests became more like mature forest with increased time since regeneration. Within all three age-classes there was a gradient in forest composition associated with distance away from the mature forest edge. This gradient included a decline in total species richness, diversity and assemblage similarity to adjacent mature forest. These trends were driven by declines in richness and cover of mature forest species. No association with distance was observed for pioneer species richness. Micro-habitat variation (influenced by proximity to mature forest) as well as differing capacities among plant species for dispersal and persistence are likely to have contributed to the observed trends. The data demonstrate the succession towards mature forest assemblages occurs more quickly in areas close to the mature forest edge compared with sites more remote from mature forest influence.

3.2 Introduction

Island biogeography theory, supported by empirical studies of islands, has established mechanisms by which isolation can be an important determinant of vascular plant diversity (MacArthur and Wilson 1967; Diver 2008; Cabral et al. 2014). Matlack (1994a) showed richness in herbs and shrubs in secondary forest declined across the

50 m spatial gradient away from old-regrowth forest edges in the Delaware/Pennsylvania Piedmont zone (USA). He also demonstrated understorey species richness was reduced in secondary forests where there was no adjacent older-regrowth forest (Matlack 1994a). Verheyen et al. (2006) demonstrated herb richness was higher in patches with greater proximity to other forest patches in Belgium. Grau (2004) also reported evidence that floristic composition of secondary regrowth in canopy gaps were affected by isolation from other canopy gaps in several disparate tropical regions of Central and South America. He concluded that the relative importance of spatial influence on floristic composition was similar to that of other environmental factors (Grau 2004).

Despite the large empirical and theoretical literature supporting island biogeography theory, limitations in the application of the theory have also been demonstrated. The fragmentation and connectivity literature address some of these limitations. For example communities and species populations can be impacted through time by the direct and indirect effect of the creation of edges within fragmented habitat (Turner 1996; Saunders et al. 1999; Laurance 2008). The impacts on species also varies greatly in response to the quality of the adjacent matrix through space and time the matrix may affect population migration and mortality rates (Tischendorf and Fahrig 2000a, b; Laurance 2008; Auffret et al. 2015). Another limitation of Island biogeography theory relates to the importance of habitat quality and structural characteristics, which may over-ride the importance of patch size for many species (Le Roux et al. 2015).

The term 'forest influence' may be applied to any mechanism driven by proximity to forest that may result in an effect on adjacent areas (Keenan and Kimmins 1993; Baker et al. 2013b). Baker et al. (2013b) demonstrate that the retention, protection and rehabilitation of mature forest patches in native forest regions may positively benefit the reestablishment of biota within silvicultural regrowth forest.

Comparisons of plant communities in wet eucalypt forest in clear-felled coupes with equivalent aged wildfire sites demonstrate some compositional differences due to harvesting. The frequency of epiphytic ferns, tree ferns and at least two trees species was reduced in clearfell sites while the frequency of weeds and sedge species

increased (Hickey 1994; Ough and Murphy 1996; Ough 2001; Turner and Kirkpatrick 2009). However both treatments give rise to communities with much lower rainforest species abundance than pre-disturbance old growth forest (Hill and Read 1984; Jordan et al. 1992; Hickey 1994; Turner et al. 2011). With improved knowledge about the limits of mature forest influence on regrowth forest biota it may be possible to mitigate silvicultural impacts on communities by reconfiguration of the harvesting system (Mitchell and Beese 2002; Gustafsson et al. 2012; Fedrowitz et al. 2014).

There are several mechanisms by which the proximity of mature forest might influence regeneration processes within secondary forests (Baker et al. 2013b). Availability and proximity to sources of propagules is one mechanism that island biogeography theory suggests is likely to be fundamental in influencing the successional trajectory of secondary forests. However, Turner et al. (1997) found that after the 1988 wildfires in Yellowstone National Park the early colonization by vascular plants was unrelated to distance from unburnt forest patches. They observed instead that in the wake of disturbance there was a high proportion of resprouting species that led to a rapid re-establishment of forest communities resembling their former composition. Within Australian wet eucalypt forests, many pioneer and rainforest species may also be insensitive to the effect of distance from propagule sources. Many are known to recover from fire vegetatively, while others have seed protected from the effects of fire by woody capsules or soil. Wind and vertebrate vectors may be able to distribute propagules over sufficient distances that the availability of a local sources may be relatively unimportant (Barker 1991; Jordan et al. 1992). Nevertheless, Hill and Read (1984) observed that the recovery of some sclerophyll and rainforest species after wildfire appeared to be limited by the proximity of seed sources.

In one of the few Australian studies focused on plant responses to mature forest influence (*sensu* Baker et al. 2013), Tabor et al. (2007) investigated the influence of proximity, direction and height of mixed forest on the establishment of four rainforest tree species in silvicultural regrowth eucalypt forest aged less than 22 years. They discovered that there was an exponential decline in the frequency of the four rainforest trees within 200 m from the mature forest edge. The rate of decline was less for species with seed traits enabling long-distance dispersal or a soil-stored seed bank.

The effect of distance on some tree species appeared to strengthen with regrowth age, but could not be distinguished from environmental differences between sites because only five sites were studied (Tabor et al. 2007).

This chapter investigates assemblages of all vascular plant species along a 200 m gradient in distance from the mature forest edge (DMFE) sampling 15 silvicultural sites in three age classes (~7, ~27 and ~45 years following clear-felling). It addresses the following five related questions:

1. Is floristic variation (assemblage, richness and diversity) of regrowth forest associated with DMFE? If so, ...
2. Is the floristic association with DMFE driven by both pioneer and rainforest species?
3. Does the strength of association with DMFE vary among plant persistence and dispersal classes?
4. What is the response magnitude of the floristic association with DMFE and does the magnitude vary in response to other environmental predictors and the importance of rainforest species in the adjacent mature forest?
5. What is the estimated depth of mature forest influence (DFI) for species assemblage?

For the purposes of this chapter it is hypothesised that proximity to mature forest has an influence on the floristic composition of regrowth wet eucalypt forest, which is driven by rainforest species more common in mature forest compared with silvicultural regrowth. From here on, this group of rainforest species are referred to as mature forest indicator species (MFI species). It is expected therefore that richness and cover of MFI species will be positively associated with DMFE. If this relationship is due only to propagule supply then it is likely there will be no differences observed with time. It is expected that pioneer species most common in silvicultural forest (silvicultural forest indicators: SFI) will have a negative association with DMFE due to competitive exclusion. It is also hypothesised that rainforest species with limited dispersal will be more dependent on mature forest influence for their establishment.

3.3 Methods

3.3.1 Data collection

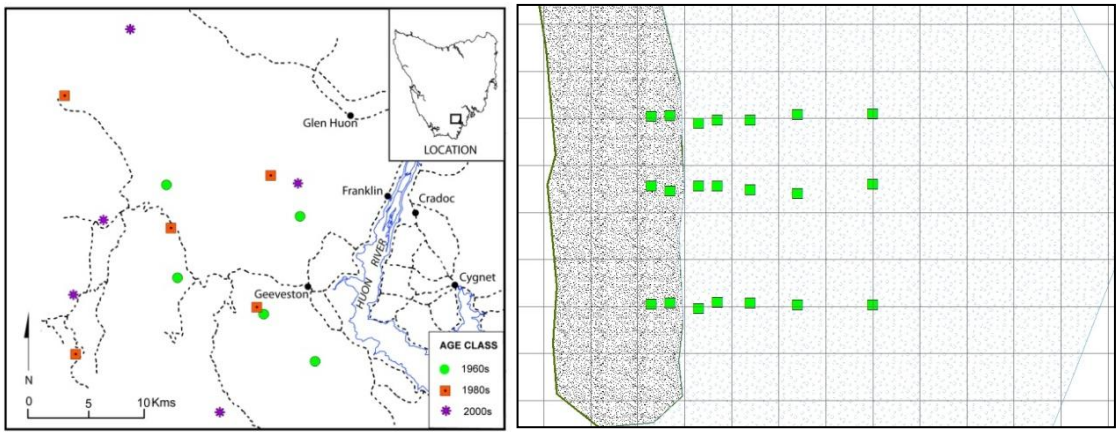


Figure 3-1. Location and age class of 15 study sites (Left) and a stylized example of sampling design showing plots located at 7 distances along each of three transects perpendicular to the boundary between mature forest (darker shading) and the silvicultural regrowth coupe (light scattered trees) with a 50 m grid superimposed for scale.

Surveys were undertaken in 2011 at 15 sites with tree height potentials of 34 m or taller within a lowland area of Tasmania's Southern Forests. Five sites in each of three regeneration age classes of wet eucalypt forest silvicultural regeneration were chosen to represent stages in the early structural development of regrowth eucalypt forest (Figure 3-1). Young regrowth was ~ 7 year old vegetation (regenerated 2002–2007), which was relatively low and open. Mid-stage regrowth was ~ 27 year old forest (regenerated 1983–89) with a closed eucalypt canopy and dense ground layer. Late-stage regrowth was ~ 45 year old forest (regenerated 1966–1970) in which strata were well separated, gaps were developing in the emergent upper eucalypt canopy, and the sub-canopy of smaller trees or tree-ferns was well developed above an open ground layer. All sites had been subject to the silvicultural treatment of clear-fell harvest followed by an intense regeneration burn. Eucalypts were regenerated either from natural seed fall from trees deliberately left standing (some 1960s sites) or from aerially sown seed. The silvicultural treatment did not involve any other active intervention in the natural regeneration process.

All potential sites had the following attributes:

- adjacent mature forest with rainforest species abundant in the understorey (i.e. mixed forest);
- an unambiguous border with mature forest of sufficient length to place three 200 m long transects at least 60 m apart, perpendicular to the mature forest edge;
- no transect less than 200 m from any other mature forest edge;
- at least 5 km between sites in the same age class.

GIS queries were used to identify available sites within each of the age and geographic classes, but were few in number in most cases. Potential sites were visited in order of maximum spatial separation but otherwise arbitrary order and the first to meet the selection criteria were accepted for study, and the remaining candidates sites discarded without being visited. Due to difficulty finding suitable late-stage regrowth sites one site pair from different age classes was separated by only 600 m at their closest points. Along each of the three transects, seven ten by ten metre plots were established at seven distances from the mature forest edge (-35, -15, 15, 35, 70, 120 and 200 m). The plot edge parallel to the transect, was offset from the transect line by up to 10 m either side, with the off-set distance and perpendicular direction (left or right of transect) determined using randomly generated integers between 1 and 10 and 1 and 2 respectively. In a few instances a plot position was moved by up to ~ 10 m closer to or further from the boundary to avoid logging tracks or streams.

For each plot the percentage projected foliage cover was estimated for all vascular plant species present. Plants derived from vegetative regeneration were noted as ‘Coppice’. The ephemerally apparent species such as orchids were excluded from all data sets and all calculations.

The field methods, calculations and data sources for the site environmental data are provided in the supplementary methods (Appendix 3.1).

3.3.2 Statistical analysis

3.3.2.1 Is floristic variation of regrowth forest associated with DMFE?

To assist in the visualisation of floristic association with DMFE a non-metric multiple dimensional scaling ordination was undertaken using PCOrd 6.08 (McCune and Mefford 2011). For this purpose the data for three distance groups were averaged such that each site was represented by a mature forest plot (-15 and - 35 m DMFE), a close regrowth plot (15 and 35 m DMFE) and a far regrowth plot (120 and 200 m DMFE). The ordination was based on the square root transformed data and a Bray-Curtis resemblance matrix. Results of this analysis are reported in the supplementary results (Appendix 3.2.1).

Three response variables were calculated for testing association of floristic composition with DMFE (Table 3–1).

Table 3-1. Floristic response variables calculated for each plot, together with their method of calculation and the test used to measure their association with distance from the mature forest edge (DMFE).

Response variables	Calculation method	Statistical Test
Assemblage	Bray-Curtis resemblance matrix of square-root transformed regrowth plot data	PERMANOVA using Primer 6.0
Total species richness	The total number of vascular plant species within the plot excluding ephemerally apparent species such as orchids	Linear Mixed Effect models using gamlss 4.3-0 specifying a normal family distribution
H'	Shannon's diversity index calculated in PCOrd 6.08 from species cover data excluding ephemerally apparent species using the formula $H' = -\sum_i^s (p_i \log\ p_i)$ where pi = importance probability in column i and matrix elements are relativized by row totals (Greig-Smith 1983, p. 233)	

Mature forest influences some aspects of the regrowth site environment through its capacity to moderate micro-climates by shading and buffering regrowth forest from wind and as a source of the relatively cool moist air in summer. However some aspects of environmental variation will not be caused by mature forest influence and could either obscure or confound floristic responses to mature forest influence. For this reason statistical methods that enabled environmental covariates to be accounted

for were chosen so that the importance of environmental variation along the gradient in DMFE could be evaluated in more detail.

Distance based linear modelling (DistLM) with the step-wise option and R-squared as the measure of best fit (Anderson et al. 2008) was used to select environmental predictors most associated with regrowth forest assemblage variation. The nested structure in the sampling design was not accounted for in the DistLM procedure but was accounted for. The co-linearity of selected predictor variables were tested using Spearman's correlation. DistLM was undertaken in Primer 6.0 (Clarke and Gorley 2006). Scatter plots and correlation matrices for the selected environmental variables are provided in the supplementary results (Appendix 3.2.1.2: Table 3–B & Figure 3–B). The final group of selected continuous environmental predictors provided the predictors from which all modelling was developed. In addition four other predictors were used – the relative cover of MFI species within the adjacent mature forest plots (MFIspp cover in MF plot); the environmental dissimilarity between the plot and the average environment of its two nearest mature forest plots (Env.Dis MF plot); the factor coppice (presence in the plot of rainforest trees recovering vegetatively) and the factor fire frequency (two levels: one or more than one disturbance event since 1890). Env.Dis MF plot was generated by importing environmental data for the variables most associated with the full floristic data set and using Principal Component Analysis to reduce these into three dimensions. The three principal components were then imported and a relative Euclidean distance matrix created to determine the environmental distance between each pair of plots. The dissimilarity of each regrowth plot its nearest two mature forest plots was then averaged to provide the average environmental dissimilarity to adjacent mature forest.

PERMANOVA was used to determine if the *a priori* groups 'DMFE class' and 'age class' of the silvicultural regrowth explained variation in the Bray-Curtis resemblance matrix. The highest ranking environmental variables were included as covariates in the model together with the fixed effect of the factor age class, the random effects of site (nested in age) and transect (nested in site), after which the fixed effects of distance and the interaction between age and distance were tested. The model is a random block design since only one sample was taken at each distance from the boundary per transect. Parameters in the initial model not achieving the alpha

significance level of 0.05 were iteratively excluded in order of highest to lowest *P*-value. The final model included only parameters with a *P*-value of < 0.05. Sums of squares were calculated using the TYPE I (sequential) method recommended for unbalanced data sets that result from the incorporation of covariates but the results were compared with those using the TYPE III (partial) method to ensure that the results were stable under both methods. A reduced model using 9999 permutations of residuals was adopted for testing all models. The PERMANOVA assumption of equal dispersion among the fixed factor groups were tested using permutational analysis of multivariate dispersions (Anderson et al. 2008). The reported *P*-values for PERMANOVA and all other statistical modelling are rounded to four or fewer decimal places, hence a reported value of $P = 0.0000$ actually represents $P < 0.00005$.

Linear mixed effect models were iteratively developed using gamlss 4.3−0 (Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007; Stasinopoulos et al. 2014) within the R software platform (R Core Team 2014) and took into account the nested structure of the data by including sites as a random factor. For a detailed account of the model selection process see Supplementary methods in Appendix 3.1 and for the model development steps for each response variables see Appendix 3.2.2. The gamlss package was chosen because it accommodates a wide range of distribution families including beta. The procedure involves internal transformation of data and provides summary outputs in the transformed scale. The function 're ( )' was used to call on the lme function from the R package nlme to enable the specification of random effects (Pinheiro et al. 2014). The software uses a maximum (penalised) likelihood estimation method using the RS algorithm. This is a generalization of the algorithm used by Rigby and Stasinopoulos (1996a, 1996b), which does not use the expected values of the cross derivatives. The theoretical justification for the method is described by Breslow and Clayton (1993). The default link functions were used for the distribution families specified. In the case of the beta distribution (variables confined to the interval between 0 and 1) the logit link function was the default for both mu and sigma. For beta distributed response data, sigma, more usually referred to as precision coefficient or phi, is used to model non-uniform variance in the response associated with predictor variables.

3.3.2.2 Is the floristic association with DMFE driven by both pioneer and rainforest species?

The allocation of species to rainforest or pioneer classes was based on average cover data from five subplots (10 x 10 m) in 107 plots (50 x 50 m) located across the study region. A plot in each mature forest and regrowth forests at the 15 sites used for the current study were represented in the 107 plot data set, ensuring all species in the current data set were represented in the larger one. Indicator species analysis (Dufrene and Legendre 1997) within the software package PCOrd 6.08 (McCune and Mefford 2011) was used to allocate species as either mature forest indicators (MFI) or silvicultural forest indicators (SFI) when their distribution across forest age classes differed at the 0.1 alpha level of significance. The use of a *P*-value of less than 0.1 was necessary to ensure a sufficient sample size. The list was similar to that of Jarman et al. (1984). Species with distributions that could not be distinguished from chance variation ($P > 0.1$) were assigned as 'other rainforest' or as 'other pioneer' species based on personal judgement of their population distribution within the lowland wet eucalypt forest communities of this region and were allocated following the list of rainforest species by Jarman et al. (1984).

Indicator species analysis was also used to determine which species within the assemblage were most associated with two classes of DMFE (near comprising plots at 15 and 35 m DMFE, and far comprising plots at 120 and 200 m DMFE). The data set for this comprised the untransformed regrowth plot data set, and excluded plots from 70 m DMFE. Only species achieving an alpha level of significance of less than 0.05 were identified as indicators of the two DMFE classes. The number of species categorised as rainforest that were more frequent in near plots versus far plots was compared with pioneers and tested with chi-square to determine if they differed more than expected by chance variation.

To determine if pioneer or rainforest species were driving species richness and species diversity responses to DMFE the richness and relative cover was calculated for each of four species groups: MFI species, other rainforest species, SFI species and other pioneer species. Linear mixed effect models including only the predictor DMFE were compared with null models to determine the strength of association among these four

plant species groups. Full linear mixed effect models were then developed from the environmental predictors for MFI species cover and MFI species richness to further explore the relationship of floristic response to DMFE and other environmental variables (for model development steps see Appendix 3.2.2.2 and Appendix 3.2.2.3 respectively). Model results are reported in Appendix 3.2.2: Table 3–C.

3.3.2.3 Does the strength of association with DMFE vary among plant persistence and dispersal classes?

Relative richness of pioneers and rainforest species in each of five persistence and dispersal classes was calculated. Each plant species was allocated to only one class. The data were relativised by dividing richness in each class by total number of species present in the group. Linear mixed effect modelling, with random effects specified for sites, was used to test the association of each response variable with DMFE, age and their interaction, specifying a normal family distribution. Non-significant model terms (P-value < 0.05) were dropped to produce the best model from these two predictors. Models of DMFE only and null models were compared using difference in Bayesian information criterion (BIC) scores to assess the relative strength of association between DMFE and each trait group; a lower BIC score indicates a better model.

3.3.2.4 What is the response magnitude of the floristic association with DMFE?

The magnitude of mature forest influence was tested on three response variables (Table 3–2). MFI species richness and cover were likely to be floristic variables responding most strongly to DMFE. The dissimilarity to mature forest was chosen because it was considered likely to provide a more direct measure of the influence exerted by adjacent mature forest on regrowth assemblage. Two measures of dissimilarity were investigated but only the Bray-Curtis dissimilarity matrix for square root transformed cover data are presented. Linear mixed effect modelling (see section 3.3.3.2) was used to develop full models of each response variable. The model development steps are described in Appendix 3.2.2.1 to 2.2.2.3, and results are presented in Appendix 3.2.2: Table 3–C.

The alternative modelling approach of non-parametric finite mixtures modelling (gamlssNP) in the package gamlss (Stasinopoulos and Rigby 2007; Stasinopoulos et al. 2014) was also used. This software was derived originally from GLIM4 macros written by Murray Aitkin and Brian Francis. The method is described with examples in Aitkin et al. (2005) and its usage justified when it is inappropriate to fit a single mean estimate for the response variable because of large, non-normal variance in the random effects of subjects (sites), suggesting the presence of sub-populations and when the alternative approach of specifying the subjects as a fixed effect precludes the examination of other predictors. Using this modelling approach the fixed effects of two or more site groups were included in the mixed effect model.

Table 3-2. Response variables used to test magnitude of floristic response to DMFE.

Response variables	Calculation method	Distribution family for modelling
Dissimilarity to mature forest	The average of the floristic dissimilarity scores for the two nearest mature forest plots using the Bray-Curtis dissimilarity matrix from square root transformed species cover data	Normal
MFI species cover	The sum cover of all mature forest indicator species within each plot as a proportion of the cover of all understorey species multiplied by 0.9999	Zero inflated beta
MFI species richness	The number of species occurring within each plot allocated as mature forest indicator species	Poisson/Normal

Fitted values extracted for the best finite mixtures model for each response were used to extract the modelled responses for all three variables at the sampled sites. The fitted values were remodelled as a generalised linear model specifying the site groups as a fixed effect. These fitted values from the new models had a correlation with the original modelled values close to one. The function 'predict' in gamlss enabled the extrapolation of the generalised linear model to predict new values of the response variables at specified values for other predictor variables within the sampled range (Chambers and Hastie 1992). The term.plot function was used to generate predicted responses across the sample range of each predictor term in a general linear model, based on the best mixed effect model but specifying the sites as fixed effects. Some of these data were graphically represented using the wireframe function from the lattice software package (Sarkar 2008).

3.3.2.5 What is the estimated depth of mature forest influence for species assemblage?

The depth of mature forest influence (DFI) is defined as the DMFE where the vascular plant assemblage of regrowth forest reached the dissimilarity to mature forest of 95% (i.e. only 5% commonality). DFI for each age class was estimated using non-linear canonical analysis of principal coordinates (NCAP) analysis constrained by distance of the sample from the mature forest edge. This followed the example provided by Miller et al. (2005) using a logistic function to fit the distance gradient given by the formula: $g(bx) = \exp(bx)/(1+\exp(bx); b > 0$, where x is the distance from the boundary such that positive values are in the direction of the silvicultural regrowth. The maximized estimates for b varied a small amount depending on the number of canonical axes which were chosen such that the total R-squared statistic was optimized. The NCAP was performed using 9999 randomizations on a Bray-Curtis resemblance matrix of square root transformed plant cover data for each age class. NCAP was conducted in R version 3.02 (R Development Core Team, 2013) using code available from https://www.stat.auckland. ac.nz/ ~millar/NCAP/NCAP.html.

To determine if the presence of coppice affected the DFI, it was recalculated for each age-class after removing plots that included rainforest species coppice. To determine whether the pioneer species occurring in the mature forest patches were influencing the depth of mature forest influence, it was recalculated for a combined data set of late and mid-stage sites comprising only MFI species covers.

3.4 Results

3.4.1 Is floristic variation in regrowth forest associated with DMFE?

There was strong evidence that the fixed effect for the factor DMFE was associated with variation within regrowth forest assemblages (Table 3–3). The fixed effect of regrowth age class was also demonstrated to be associated with assemblage variation but there was no evidence for an interaction between age and DMFE. In other words, assemblages varied in association with DMFE classes for all three age classes. Seven environmental variables were successfully fitted in the model as covariates (*P* all < 0.04, Table 3–3). The results for DMFE were similar when environmental covariates were excluded (data not shown). There was evidence from pairwise contrasts among the DMFE classes that assemblages from both 15 m and 35 m differed sufficiently from those at 200 m DMFE to be distinguishable from chance variation ($P < 0.05$). No other contrasts achieved an alpha level of significance (*P*-value all > 0.05).

Tests of dispersion confirmed there was homogeneity of dispersion between each distance class when all silviculture regrowth plots when examined together ($F = 0.3$, df1 = 4, df2 = 220, $P = 0.91$). Furthermore, there were no differences in dispersion between distance classes in any of the age classes when analysed separately. However dispersion was not homogenous between age classes ($F = 26.5$, df1 = 2, df2 = 220, $P = 0.00010$). Dispersion was greatest for mid-stage classes (n = 75, Mean dispersion = 41.6, SE = 1.1) and least for young regrowth (n = 75, Mean dispersion = 38.4, SE = 0.9). All pairwise contrasts provided evidence of differences greater than would be expected by chance variation (t all > 2.18, *P* all < 0.05). Dispersions were also found to vary between sites in young and mid-stage age regrowth forests (young: $F = 6.3$, $P = 0.0006$, mid: F = 5.6, $P = 0.001$), but not in late stage regrowth ($F = 1.8$, $P = 0.21$).

Table 3-3. Results of PERMANOVA, modelling species assemblage variation in response to distance from the mature forest edge (DMFE), regrowth forest age and other site covariates.

Source	df	SS-Type I	MS	Pseudo-F	*P*-values	SqrtCV
Covariatiates:						
Soil C/N ratio	1	53138	53138	7.92	0.0001	14.9
Radiation in Lowest Week	1	30104	30104	3.16	0.0004	13.3
Soil pH	1	35517	35517	5.74	0.0001	11.4
Mean daily VPD in April	1	23715	23715	2.71	0.0038	10.4
Temp seasonality	1	33018	33018	2.84	0.0004	10.0
Northwestness Index	1	12595	12595	2.08	0.0246	6.5
Mean daily Temp in April	1	16219	16219	1.93	0.0365	6.0
Factors:						
Age [fixed]	2	55592	27796	2.86	0.0002	19.5
Site (in Age)	12	91724	7644	5.62	0.0001	25.7
Transect (in Site in Age)	30	45218	1507	1.80	0.0001	11.9
DMFE [fixed]	4	6377	1594	1.90	0.0004	4. 5
Residuals	169	141840	839			29.0
Total	224	545060				

Abbreviations: Df: Degrees of freedom; SS: Sum of Squares- Type I (sequential); MS: Mean Square; *P*-value: Probability based on permutations calculated from more than 9901 permutations and rounded to four decimal places; SqrtCV: Square root of the estimated Components of Variation; CN: carbon nitrogen ratio; VPD: Vapour Pressure Differential; Temp: Temperature. Note that all factors in the model were specified as random unless otherwise indicated as fixed.

DMFE was negatively associated with both species richness and Shannon's H (Figure 3–2, Table 3–4). Log transformation of DMFE provided a marginally poorer model fit compared with untransformed DMFE for both responses. The full model for species richness provided evidence of a three order polynomial association between species richness and age, a positive association with rainfall in the warmest quarter, and a negative association with aspect, which demonstrated that richness increased in higher rainfall, southerly aspects and that it was lowest in the mid-stage age class and at greatest DMFE. Diversity had a complex, non-linear relationship with climate and topographic variables (Table 3–4).

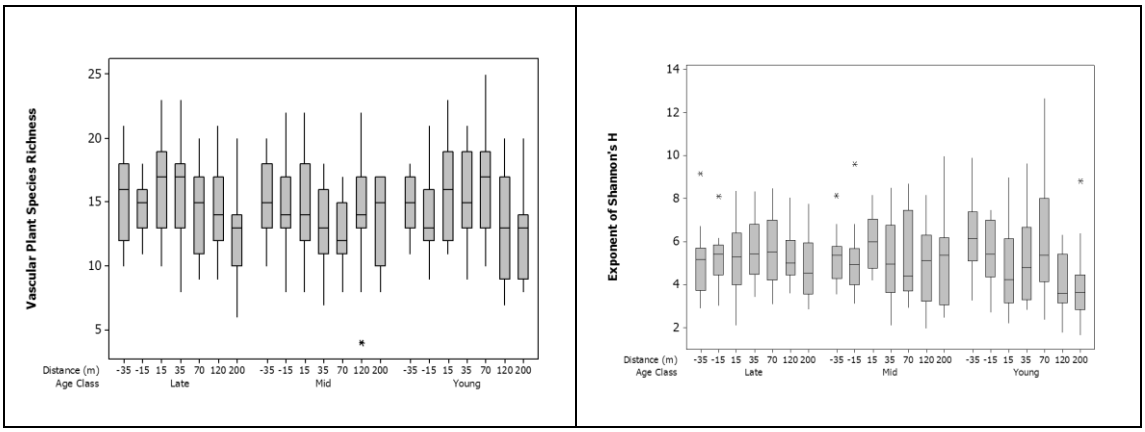


Figure 3-2. Box plots showing mean and standard deviation of total species richness (left) and Shannon's diversity index scores (right) for each age class with Distance to mature forest edge (DMFE)

Table 3-4. Gamlss linear mixed effect model results for Species richness and Shannon's H'.

Species richness			**Shannon's H'**	
	(family = normal distribution)	Null model BIC = 1246.0 R = 0.510	(family = normal distribution)	Null model BIC = 194.0 R = 0.521
model terms		DMFE model		DMFE model
DMFE	t = -3.99 (*P* = 0.0001)	BIC = 1230.4 R = 0.557	t = -3.17 (*P* = 0.0018)	BIC = 184.0 R = 0.551
	Difference between DMFE & null model:	**BIC Δ = 15.6 R Δ = 4.7**		**BIC Δ = 10.0 R Δ = 0.03**
	Fixed effects Full Model for Mu:	BIC = 1183.4 R = 0.515	Fixed effects Full Model for Mu	BIC = 157.4 R = 0.587
Mu Intercept	0.6332 ± 0.5141 t = -1.23 *P* = 0.2195		-1.4659 ± 0.5479 t = -2.68 *P* = 0.0081	
DMFE	-0.0124 ± 0.0033 t = -3.75 (*P* = 0.0002)	BIC Δ = 9.8 R Δ = 0.058	-0.0010±0.0003 t = -3.23 (*P* = 0.0014)	BIC Δ = 10.4 R Δ = 0.027
Rainfall in warmest quarter	0.0376 ± 0.0091 t = 4.14 (*P* = 0.0000)	BIC Δ = 33.4 R Δ = -0.035	0.0065±0.0014 t = 4.47 (*P* = 0.0000)	BIC Δ = 13.5 R Δ = -0.007
Cos Aspect	-1.3610 ± 0.3946 t = -3.45 (*P* = 0.0007)	BIC Δ = 27.1 R Δ = -0.020	0.1108±0.0519 t = 2.14 (*P* = 0.0339)	BIC Δ = 3.6 R Δ = 0.018
Northwestness Index			-0.9123 ± 0.2400 t = -3.80 (*P* = 0.0002)	BIC Δ =14.5 R Δ = 0.036
Mean daily minimum temperature January			0.1373 ± 0.0565 t = 2.43 (*P* = 0.0160)	BIC Δ = 6.5 R Δ = 0.000
Age (1st order polynomial)	7.5642 ± 3.5982 t = 2.10 (*P* = 0.0368)	BIC Δ = 33.9 R Δ = -0.032		
Age (2nd order polynomial)	9.4924 ±3.4400 t = 2.76 (*P* = 0.0063)			
Age (3rd order polynomial)	-8.3455±3.5007 t = 2.38 (*P* = 0.018)			
	Difference between full & null model:	**BIC Δ = 62.7 R Δ = 0.005**		**BIC Δ = 36.6 R Δ = 0.066**

3.4.2 Is the floristic association with DMFE driven by both pioneer and rainforest species?

Species within the regrowth forest assemblage that were most associated with close plots (15 m and 35 m DMFE) were all rainforest trees, which were included also among the list of MFI species. In order of indicator value (IV) they were: *Nothofagus cunninghamii* (IV = 44, *P* = 0.01), *Atherosperma moschatum* (IV = 34, *P* = 0.003), *Tasmannia lanceolata* (IV = 22, *P* = 0.013), *Anodopetalum biglandulosum* (IV = 19, *P* = 0.047) and *Phyllocladus aspleniifolius* (IV = 19, *P* = 0.043). Only one SFI species, the tree *Monotoca glauca,* was identified as an indicator for far plots (120 m and 200 m DMFE, IV = 45, *P* = 0.03).

Collectively, mature forest species (including MFI species) were more frequent in the near plots than the far plots (n = 40, df = 1, Chi-Sq = 36.1, *P* = 0.000). In contrast, the frequency of pioneer species (including SFI) were no more likely to occur in the far plots than near plots (n = 61, df = 1, Chi-Sq = 1.328, *P* = 0.249). The difference in distribution of these two species groups was unlikely to have resulted from chance variation (Chi-Sq = 31.72, df = 1, *P* = 0.000, Table 3–5). These results support the hypothesis that it is mature forest species driving the assemblage association with DMFE and not pioneer species.

Table 3-5. Number of species more frequently found in near versus far plots by whether they are rainforest or pioneer species. Note the subset of indicator species numbers are listed in parentheses.

	Most frequent in Near plots	Most frequent in Far plots	Species totals
All pioneer species (SFI species)	26 (6)	35 (11)	61 (17)
All mature forest species (MFI species)	39 (31)	1 (0)	40 (31)
Subtotal of species frequencies (indicator species)	65 (37)	36 (11)	Total 101 (Total 48)

Linear mixed effect models for both the cover and richness of MFI species improved with the addition of the fixed effect term DMFE compared with null models for mu (Table 3–6). This provided evidence that these species were negatively associated with DMFE. Other rainforest species (excluding MFI species) were also negatively associated with DMFE but this relationship was too weak to distinguish from chance variation (Table 3–6). The cover of SFI species but not their richness was positively associated with DMFE (Table 3–6). There was also weak evidence that species richness of other pioneer (excluding SFI species), but not their cover, was associated positively with DMFE (Table 3–6). These results are generally consistent with the hypothesis that rainforest species were the strongest drivers of the negative association of total species richness with DMFE, although not all rainforest species may be contributing to the observed trend, and other pioneer species appear to be weakening it (Table 3–6).

Table 3-6. Summary of linear mixed effect model of response to DMFE of richness and cover of species groups based on habitat preference.

(R= Pearson's correlation between predicted and observed values.)

Random effects:	Transects nested in sites				Model Improvement BIC (R)		Age	AGE*DMFE
Fixed effects:	Null	Log DMFE	Null	DMFE				
Species Groups	Group Cover (family Zero Inflated Beta)		Group Richness (family NO)		Cover	Richness	Group Richness (family NO)	Group Richness (family NO)
Silvicultural Forest Indicators (SFI)	BIC = -92.6 R = 0.727	t = 4.87 *P* = 0.000 BIC = -115.7 R = 0.764	BIC = 882.5 R = 0.712	t = 1.10 *P* = 0.272 BIC = 881.2 R = 0.714	ΔBIC = 23.1 (ΔR =0.037)	ΔBIC = 1.3 (ΔR =0.002)	t = -4.10 *P* = 0.001 BIC = 877.4 R = 0.710	Poly(age,2)*DMFE t = -3.06 *P* = 0.003 BIC = 863.0 R = 0.730
Other pioneers	BIC = 341.6 R = 0.579	t = 0.84 *P* = 0.401 BIC = -342.1 R = 0.584	BIC = 837.6 R = 0.571	t = 2.00 *P* = 0.048 BIC = 833.6 R = 0.582	ΔBIC = 0.5 (ΔR =0.00)	ΔBIC = 4.1 (ΔR =0.011)	t = -1.28 *P* = 0.223 BIC = 836.6 R = 0.571	t = 0.98 *P* = 0.359 BIC = 831.7 R = 0.584
All pioneers species	BIC =-339.4 R = 0.817	t = 6.31 *P* = 0.000 BIC = -373.1 R = 0.817	BIC = 1091.1 R = 0.666	t = 1.84 *P* = 0.068 BIC = 1087.5 R = 0.672	BIC = 33.7 (ΔR =0.044)	ΔBIC = 3.5 (ΔR =0.007)	t = -3.40 *P* = 0.005 BIC = 1086.5 R = 0.663	t = 1.45 *P* = 0.15 BIC = 1080.9 R = 0.674
Mature Forest Indicators (MFI)	BIC = -46.8 R = 0.770	t = -5.66 *P* = 0.000 BIC = -72.9 R = 0. 814	BIC = 1106.1 R = 0.777	t = -7.61 *P* = 0.000 BIC = 1069.4 R = 0.830	ΔBIC = 26.1 (ΔR =0.043)	ΔBIC = 54.3 (ΔR =0.053)	t = 2.53 *P* = 0.025 BIC = 1122.6 R = 0.776	t = - 0.45 *P* = 0.66 BIC = 1068.1 R = 0.830
Other rainforest	BIC = -187.1 R = 0.416	t = -0.22 *P* = 0.82 BIC = -187.1 R = 0.414	BIC = 442.7 R = 0.503	t = -1.62 *P* = 0.106 BIC = 447.2 R = 0.513	ΔBIC 0.0 (ΔR =0.002)	ΔBIC = 2.7 (ΔR =0.009)	t = -1.07 *P* = 0.31 BIC = 448.9 R = 0.503	t = -0.78 *P* = 0.43 BIC = 445.5 R = 0.513
All rainforest species	BIC = -85.2 R = 0.775	t = -5.94 *P* = 0.000 BIC = -116.3 R = 0.818	BIC = 1148.7 R = 0.765	t = -7.86 *P* = 0.000 BIC = 1094.4 R = 0.821	ΔBIC = 31.0 (ΔR =0.043)	ΔBIC = 54.2 (ΔR =0.056)	t = 2.29 *P* = 0.040 BIC = 1147.5 R = 0.764	t = - 0.61 *P* = 0.54 BIC = 1093.1 R = 0.821

3.4.3 Does the strength of association with DMFE vary among plant persistence and dispersal classes?

Richness within most persistence/dispersal classes was associated with DMFE (Table 3–7). The only classes not associated with DMFE was the rainforest species with soil stored seed (only one species, *Acacia melanoxylon*) and bradysporous and wind-dispersed pioneer species (Table 3–7). All rainforest species groups were negatively associated with DMFE, although the strength of the association varied.

DMFE was of less importance for the richness of most pioneer groups than richness of most rainforest groups. There was positive association between DMFE and richness of pioneer species with soil-stored seed and with vertebrate dispersed seed. However, pioneer fern richness was negatively associated with DMFE, although only within young-regrowth forest sites. Only the wind-dispersed pioneer angiosperm species had a polynomial relationship to regrowth age, demonstrating the greatest richness at mid-stage regrowth sites (Table 3–7).

On next page:

Table 3-7. Result summary for gamlss linear mixed effect models for relative richness of each persistence/dispersal group.

Table 3-7 definitions and notes:

Codes for *P*-values: n.s. *P* >0.1; # 0.1> *P* >0.05; * 0.05> *P* >0.01; ** 0.01> *P* >0.001; *** 0.001 > *P*

^ Best model based on BIC, subject to an alpha level of significance of <0.05 for each model term. Models were analysed specifying a normal distribution family and random effect term for sites. DMFE was either left untransformed (metric) or was log-transformed (log). First, second and third order polynomial relationships for age are listed as 1–3, respectively, where these provided a better fit than a linear term for age.

Table 3.7. For detailed explanation see previous page.

Species groups:	BIC for	Model strength	Fixed effects				Notes
Rainforest species	Null model (N.M.) DMFE model (D.M.) improvement (Δ)	Pearson's R & BIC	Intercept	DMFE^	Age^	DMFE X Age	
low dispersal /persistence n=5	N.M.= 1832.3 D.M.= 1791.3 Δ = 41.0	R:0.81 BIC:1775	36.0488±8.9080 (t = 4.05, ***)	Log -9.2797 ±1.4956 (t = -6.20, ***)	-0.5005 ± 0.3013 (t = -1.66, ns)	0.1425 ±0.0506 (t = 2.82, **)	Log decline with DMFE all ages, gradient weakens with age
spores n=18	N.M.= 1681.2 D.M.= 1658.2 Δ = 23.0	R:0.80 BIC:1645	-11.5257 ± 5.800 (t = -2.03, *)	Log -0.2172 ± 1.1298 (t = -0.19, ns)	0.9349 ± 0.1923 (t = 4.86, ***)	-0.1073 ±0.0382 (t = -2.81, **)	Log decline with DMFE all ages, gradient strengthens with age.
wind dispersed n=5	N.M.= 1960.6 D.M.= 1941.2 Δ = 19.4	R:0.72 BIC:1938	8.4777 ±7.9040 (t = 1.07, ns)	Log -5.0690 ±1.1309 (t = -4.48, ***)	0.4922 ± 0.2160 (t = 2.28, *)	ns	Log decline with DMFE all ages.
vertebrate-dispersed n=12	N.M.= 1582.0 D.M.= 1566.9 Δ = 15.1	R:0.73 BIC1562	5.7712 ±3.3929 (t = 1.70, #)	Metric -0.0490 ± 0.0129 (t = -3.81, ***)	-0.1381 ± 0.1148 (t = -1.20, ns)	0.0009 ± 0.0004 (t = 2.09, *)	Weak decline with DMFE in young and mid stage regrowth.
soil stored n=1	N.M.= 2333.7 D.M.= 2333.6 Δ = 0.1	R:0.56 BIC:2329	22.5131±10.2195 (t = 2.20, *)	ns	-0.8934 ± 0.3456 (t = -2.58, *)	ns	Decline with age only.
Pioneer species							
soil stored seed n=26	N.M.= 1347.6 D.M.= 1339.6 Δ = 8.0	R:0.72 BIC:1340 Df:16.0	-3.6931 ±1.6000 (t = -2.31, *)	Log 0.8965 ±2959 (t = 3.03, **)	ns	ns	Log increase with DMFE all ages.
vertebrate dispersed seed n=13	N.M.= 1664.4 D.M.= 1661.3 Δ = 3.1	R:0.62 BIC:1659	-5.6523 ±2.9889 (t = -1.89, #)	Log 1.3721 ±0.6082 (t = 2.25, *)	ns	ns	Log increase with DMFE in all ages.
spores n=4	N.M.= 2020.0 D.M.= 2017.0 Δ = 3.0	R:0.49 BIC:2002	20.5398 ± 6.1332 (t = 3.35, **)	Metric -0.1348 ±0.0348 (t = -3.88, ***)	-0.7039 ±0.2074 (t = -3.39, ***)	0.0041 ±0.0012 (t = 3.47, ***)	Weak decline with DMFE in young regrowth only. Weak decline with age.
wind dispersed seed n=13	N.M.= 1435.6 D.M.= 1435.4 Δ = 0.2	R:0.71 BIC:1428	0.0000 ±0.7801 (t = 0.00, ns)	ns	1:-44.7198 ±11.7012 (t = -3.82) *** 2: 24.3016±11.7012 (t = 2.08)* 3:-27.2098±11.7012 (t = -2.33)*	ns	No association with DMFE, peak richness in mid stage regrowth.
bradyspore n=5	N.M.= 1473.3 D.M.= 1473.3 Δ = 0.0	R:0.78 BIC:1473	4.7275 ±2.9541 (t = 1.60, ns)	ns	-0.1876 ± 0.0999 (t = -1.88, #)	ns	No association with DMFE, possibly a weak decline with age.

3.4.4 What is the response magnitude of the floristic association with DMFE?

PERMANOVA provided evidence that DMFE specified as a factor, accounted for only a relatively small amount of the total variation in assemblage across sampled plots (4.5% of the square root of the covariance). This was less than a quarter of the variation attributed to regrowth forest age, which in turn was less than the variation attributed to random differences between sites and the residual of unexplained variance (Table 3–3). Despite this result, there was an observable association between DMFE and several floristic response variables – particularly dissimilarity to adjacent mature forest, cover and richness of MFI species (Figure 3–3).

DMFE, regrowth age, slope, and MFI species cover in mature forest plots were also associated with all three of the response variables DMFE, regrowth age, slope, were positively associated with richness and cover of MFI species and negatively with dissimilarity to mature forest (Table 3–8). Cover of MFI species was negatively associated with soil pH. Models of the dissimilarity to mature forest and richness of MFI species were strengthened by the inclusion of an interaction term for age and DMFE, and the inclusion of age in the model for dissimilarity to mature forest was only possible with the inclusion of this interaction term. The presence of coppice was negatively associated with dissimilarity to mature forest and positively associated with MFI species cover (Table 3–8). There was also evidence that the variance of all three responses varied across the sampled range and there was some evidence that random effects of sites were not distributed normally (Appendix 3.2.2).

Part of the measured association between DMFE and the response variables was due to increasing environmental differences away from the mature forest edge (Spearman's R = 0.61, $P < 0.00001$). Nevertheless the predictor Environmental dissimilarity and DMFE were able to be fitted together in models of each response variable, without changing their direction of association (Appendix 3.2.2).

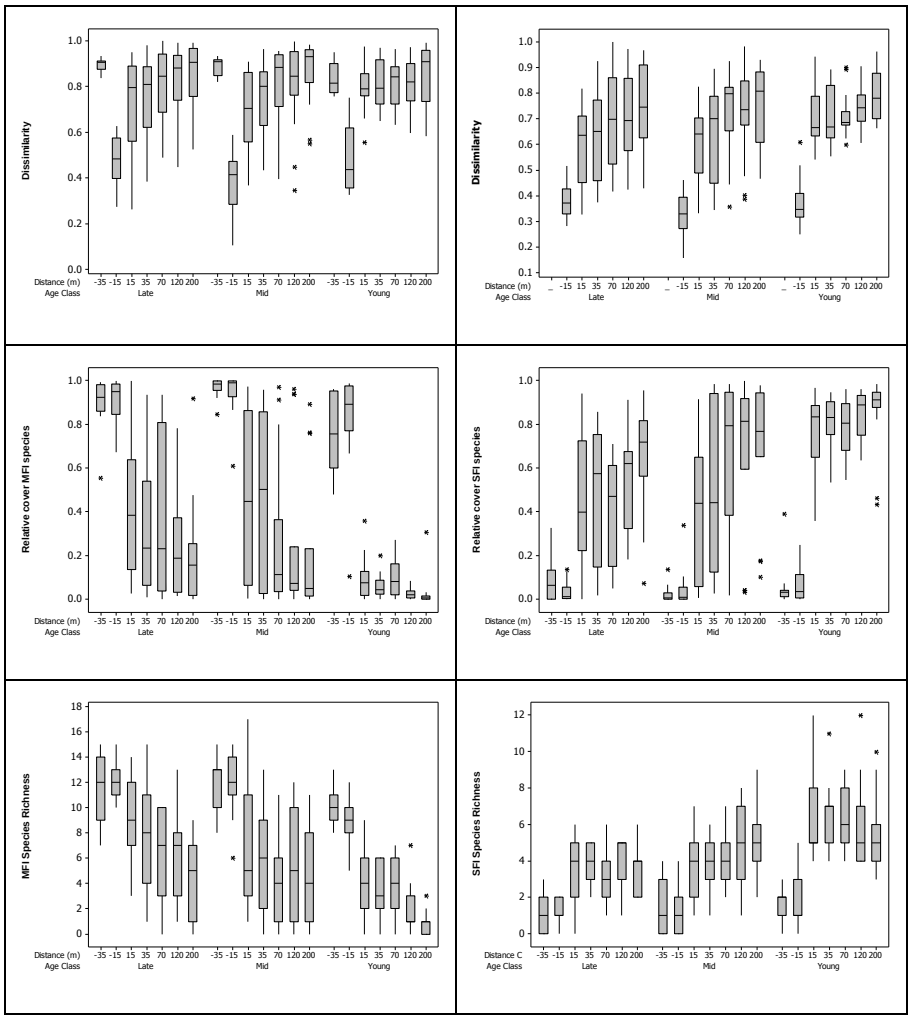


Figure 3-3. Box plots of mean and standard deviation of floristic response variables by distance from the mature forest edge within sites grouped by regrowth age classes : Relative Sorenson dissimilarity to mature forest (top left); Bray-Curtis dissimilarity to mature forest from square root transformed species cover data (top right); Cover of mature forest indicator species (centre left); Cover of silvicultural forest indicator species (centre right) and Richness of mature forest indicator species (bottom, left); Richness of silvicultural forest indicator species (bottom right).

Notes: The dissimilarity score for regrowth plots (15 to 200 m) is the mean dissimilarity to plots at -15 and -35 m on the same transect and for comparative purposes the dissimilarity between the two mature forest plots is shown at -15 m distance, and the average dissimilarity between the mature forest plots and all silvicultural forest plots is provided at -35 m.

Table 3-8. Strength of association and effect size for each fixed and random effect term in the model for mu for best Gamlss linear mixed effect models developed for three response variables: 1. Dissimilarity to mature forest (family = normal, BIC = -391, Pearson's R = 0.83) 2. Relative cover of mature forest indicator (MFI) species (family = Beta, BIC = -538, R = 0.84); 3. Richness mature forest indicator species (family= Poisson, BIC =995, R = 0.84). (Notes: see next page)

	Fixed effect terms in model for mu						Terms in Sigma model^			Random Effects
1. Dissimilarity to mature plots (Bray-Curtis)	Log DMFE	Age	Slope	Coppice (+)	MFIspp cov.mf plot	log DMFE x Age interaction	MFIspp cover mf plot			Sites
Coefficient (±Std dev)	0.0312 (±0.0097)	- 0.0053 (±0.0022)	0.0028 (±0.0008)	- 0.0875 (±0.0229)	0.1970 (±0.0548)	0.0008 (±0.0004)	1.983 (±0.3705)			
t-value	3.22	-2.44	3.69	-3.82	3.59	2.24	5.35			
P-value	0.002	0.030	0.000	0.000	0.000	0.03	0.0000			
Δ BIC	62.6	0.3	12.3	12.5	14.0	5.3	15.9			87.5
Effect Size	0.09 to 0.18	0.03 to 0.11	0.11	0.09	0.07	na	na			0 - 0.38
Predictor Range	15 to 200m	5-45 years	5 to 45%	+/-	0.6-1.0 rel.cover	na				l3-m4
2.MFI spp. cover	Log DMFE	Age	Slope	Coppice (+)	MFIspp cov.mf plot	pH	L.DMFE	Age	NWS	Sites
Coefficient (±Std dev)	-0.6401 ±0.0620	+0.0541 ±0.0193	-0.0162 ±0.0070	1.0863 ±0.1799	+1.5565 ±0.7199	-0.3686 ±0.1637	0.334 ±0.060	0.031 ±0.004	2.590 ±0.366	
t-value	-10.33	2.80	-2.30	6.04	2.16	-2.25	-5.58	8.59	7.09	
P-value	0.000	0.015	0.022	0.000	0.0318	0.0254	0.000	0.000	0.000	
Δ BIC	70.6	8.0	5.0	25.7	3.1	5.3	16.8	39.0	32.5	154.6
Effect Size	0.01 to 0.39	0.02 to 0.17	0.02 to 0.16	0.03-to0.26	0.02 to 0.15	0.05-0.18				0.24–0.76
Predictor Range	15 to 200m	5-45 years	5 to 45%	+/-	0.6-1.0 rel.cover	4.0 – 6.0				l3-m4
3.MFI spp. richness	DMFE	Age class	TIN	April Temp	MFIspp cov.mf plot	DMFE*Age C				Sites
Coefficient (±Std dev)	-0.0027 ± 0.0008	-0.829 m, -0.579y ± 0.362 m, ± 0.377y	-0.0036 ± 0.0012	-0.5397 ± 0.1757	1.989 ±.5293	0.001m, -0.004 ± 0.001m, 0.002y				
t-value	-3.49	-2.29m, -1.53y	-3.10	-3.07	3.76	1.20m, -2.75y				
P-value	0.001	0.04m, 0.15y	0.002	0.002	0.000	0.23, 0.001				
Δ BIC	26.3	1.1	9.0	8.3	14.1	13.1				162.7
Effect Size	0 to 8	0 to 7	0 to 13	1 to 11	1 to 11	na				
Predictor Range	15 to200	y/m/l	-200 to 200	9.0 to11.0	0.6 to 1.0	na				M2 /L2

Explanatory notes for Table 3–8 (see previous page):
If DMFE*Age interaction is excluded t-value for DMFE = 5.24, *P* = 0.0000;
^Terms in sigma model explain changes in the variance in the response. Positive coefficients indicate increased variance in the response for higher values of the predictor.
Abbreviations: DMFE: Distance from the mature forest edge; TIN topographic index, NWS northwestness index.
Δ BIC = (BIC for model omiting the term) - (BIC for the full model).

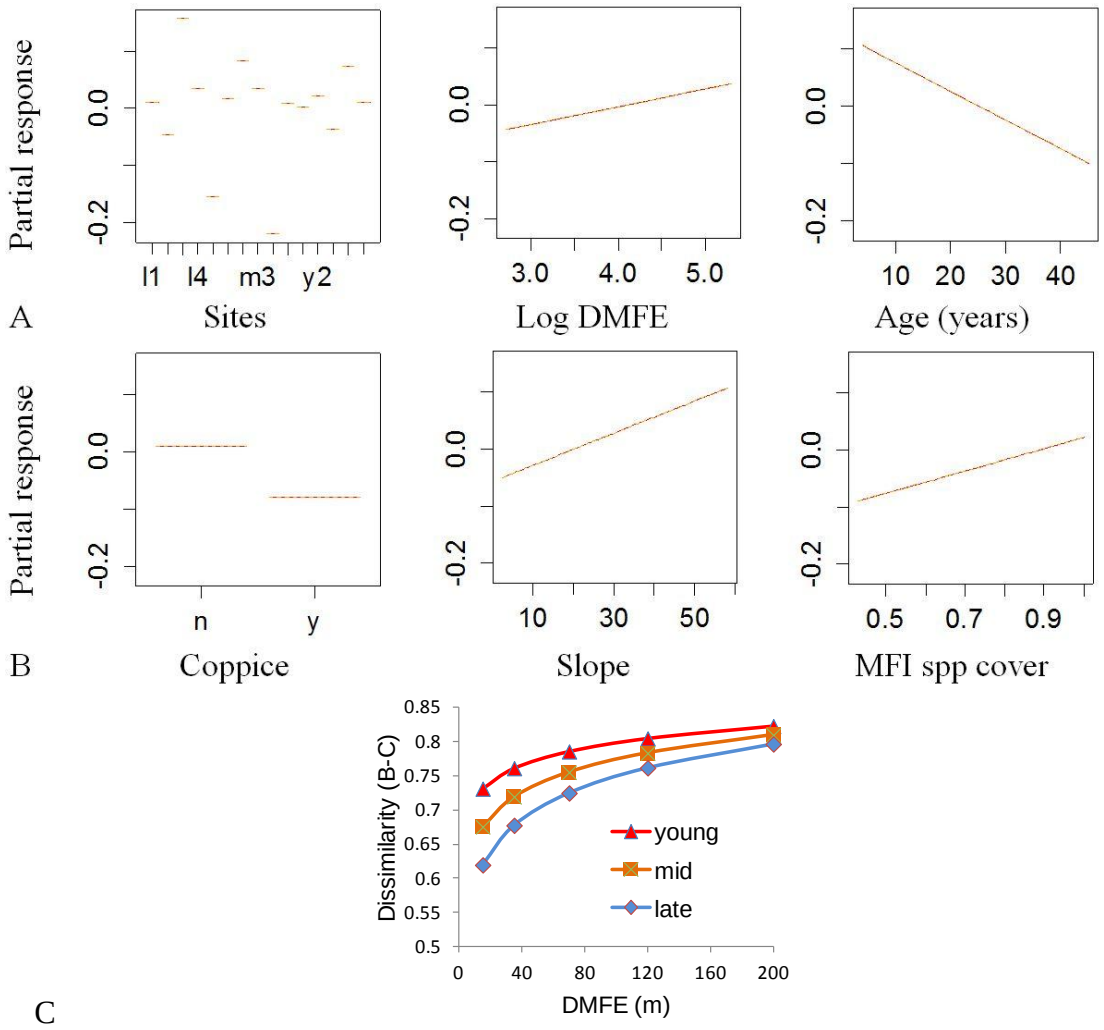


Figure 3-4. A & B: Predicted partial response of Bray-Curtis dissimilarity to mature forest to each predictor (Y-axis) across its sampled range (x-axis); C: Predicted response of Bray-Curtis dissimilarity to mature forest to the interaction between Age and DMFE.

Notes: Predictions derived from generalised linear models developed using predicted values from linear mixed effect models specifying the random effects of sites. Predictions for dissimilarity to mature forest (C) were for an average site (L2) without coppice on a slope of 20% and MFI species cover in mature forest plot of 0.95.

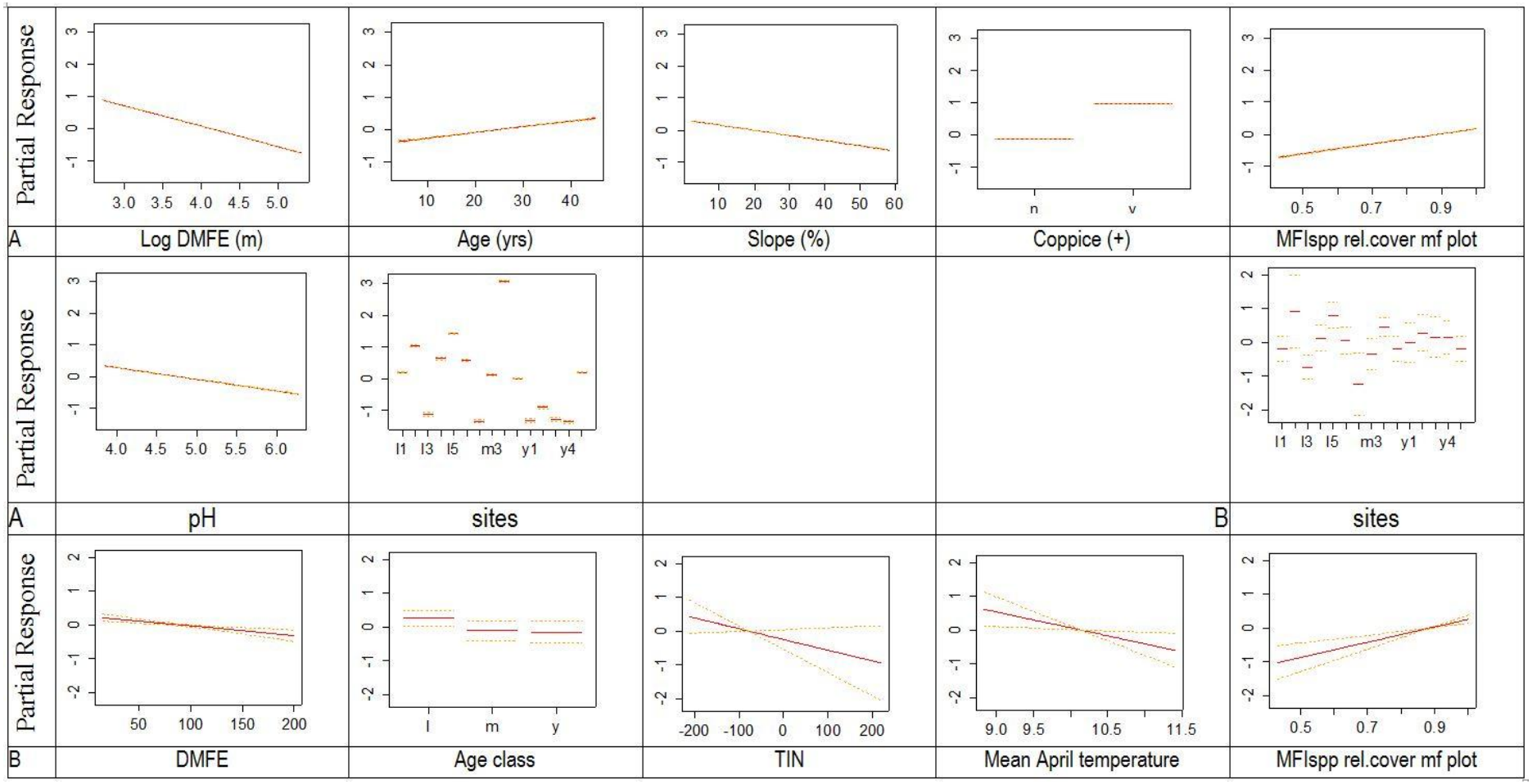


Figure 3-5. Predicted partial response to each predictor (y-axis) across its sampled range (x-axis) for A) Cover of MFI species and B) Richness of MFI species.

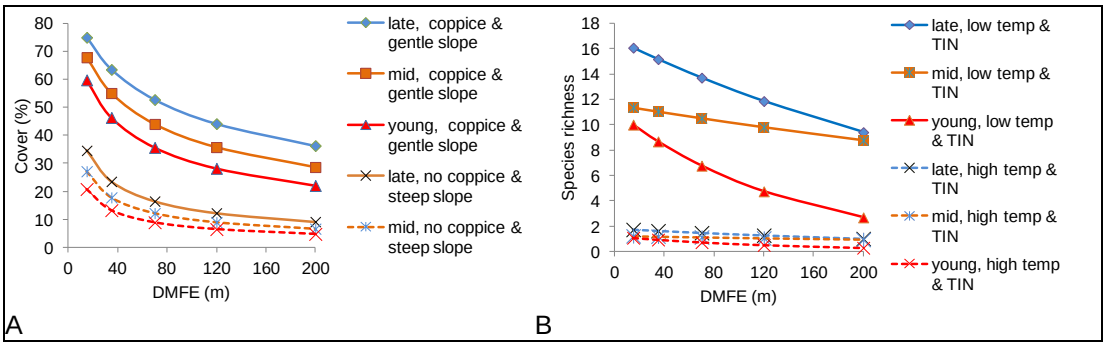


Figure 3-6. Predicted response to age and DMFE for A) cover of MFI species and B) richness of MFI species.

Notes: Cover of MFI species were estimated for an average site l1, with an average pH (0.475) and an MFIspp cover in MF plot of 0.95.
Richness of MFI species were estimated for an average site (m5) and MFIspp cover in MF plot of 0.95.

The actual effect of DMFE on the response size predicted by the modelling was in the same order of magnitude as that for other predictors across their sampled range (Figure 3-4, Figure 3-5). In all cases the predicted magnitude of the effect of DMFE varied depending on regrowth age (Figure 3-4C; Figure 3-6). At young sites there was very little variation in the predicted response across the sampled range, whereas at late-stage sites the gradient in all three responses was pronounced. Using linear mixed effect modelling, the maximum predicted change in the responses from 15 m to 200 m was 0.18 Bray-Curtis units of dissimilarity, 39% cover of MFI species and 8 MFI species. These changes were larger than predicted across the sampled range of the other predictor terms for Bray-Curtis dissimilarity and MFI species cover, but smaller or much the same as the other predictors for richness of MFI species. The predicted differences between sites were larger than those predicted for any of the predictors; and those predicted for species richness were well beyond observed differences, suggesting that the modelling results may have been compromised by the lack of normality among the random effects for sites.

Alternative modelling methods (‘finite mixtures’ and ‘lme’ with sites as a fixed factor) provided strong evidence that climatic differences explained some of the variation in responses between sites, the best predictor of which was rainfall in the warmest quarter (Appendix 3.2.2 Table 3–C, Figure 3–7). Using finite mixtures modelling the maximum magnitude of the effect of DMFE on responses was either

reduced (MFI richness and dissimilarity to mature forest) or remained the same (cover of MFI species), and was predicted to affect the responses slightly less than at least some of the other predictors compared with the predictions from LME models (Figure 3–7, Appendix 3.2.2: Table 3–C). MFI species were predicted by finite mixture models to be at their maximum richness (~15.7 species) and cover (99%) at 15 m DMFE, in late stage sites, in the most favourable situations and site types. In these situations the predicted dissimilarity scores reached their lowest levels (0.21 Bray-Curtis units). However in more average situations of slope, aspect and rainfall the richness at the boundary could vary from 8.6 to 11.1 MFI species depending on unexplained differences in sites (Figure 3-8). Unexplained site differences were predicted to affect MFI covers by up to 32% in some situations, and dissimilarity to mature forest by 0.18 Bray-Curtis units (Figure 3-8).

The variation across the distance gradient (15 m to 200 m) was predicted to be associated with a drop of 3.3 MFI species, as much as 40% cover of MFI species at young sites in the most favourable situations, and an increase in dissimilarity of 0.13 Bray-Curtis units (Figure 3-8). At 15 m DMFE succession resulted in a predicted increase of 5.2 MFI species and a decrease in dissimilarity of 0.14 Bray-Curtis units, from young to late stage regrowth.

The highest richness levels predicted by LME for an average site was 18 MFI species, compared with 16 for the more species rich site group modelled by finite mixtures. Likewise whereas the finite mixture model predicted a change of only 3.3 species between 15 m and 200 m, a drop of 7.5 species was predicted by the LME model. The predicted increase from 11.2 to 18 species from young to late-stage regrowth by the LME model was also larger than the change of 6.3 MFI species predicted by finite mixtures. Discrepancies between predictions for dissimilarity were less marked than those for models of MFI species richness (Table 3–8, Appendix 3.3.2, Table 3–C).

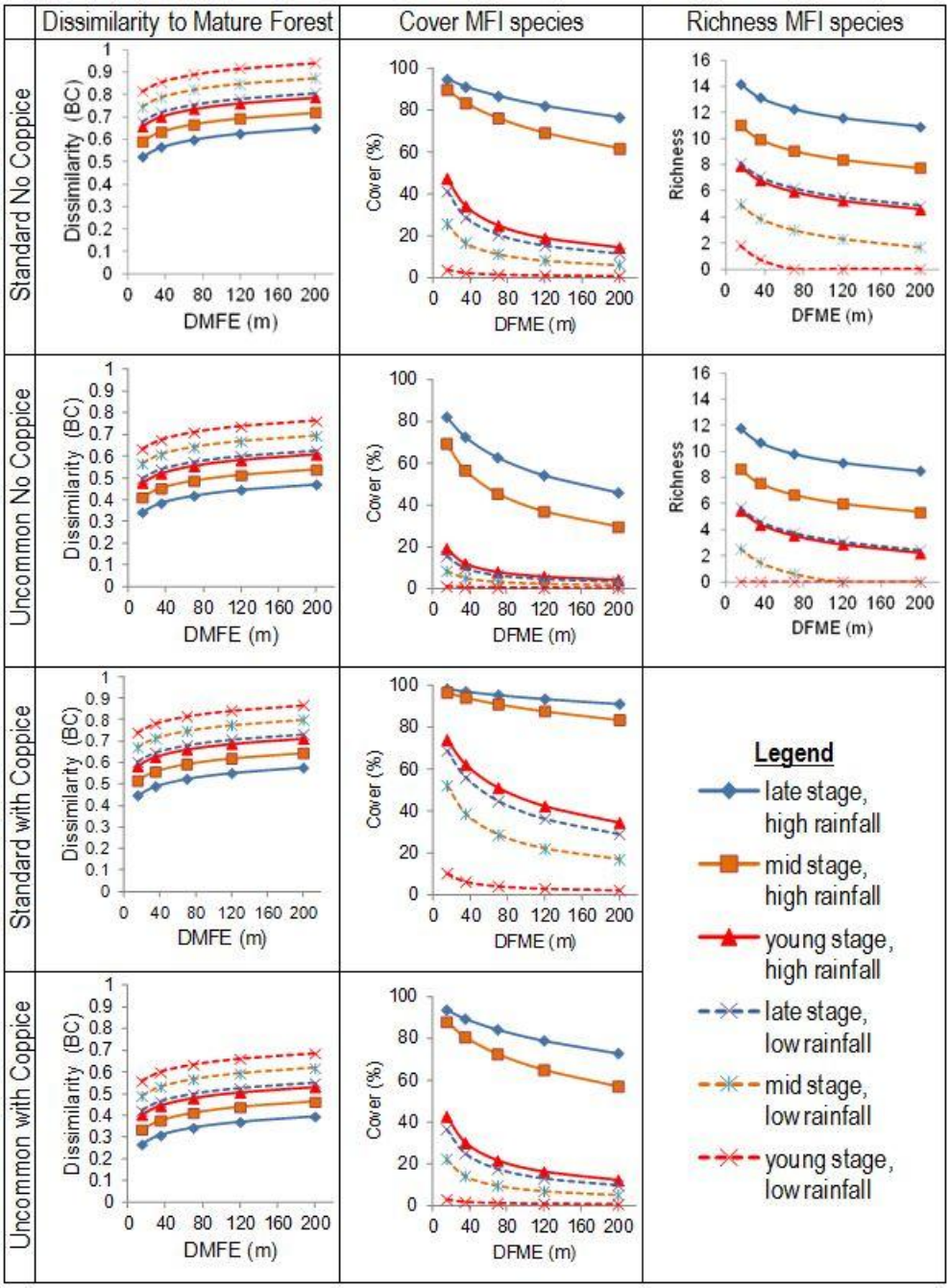


Figure 3-7. Predicted effect of variation in DMFE (x- axis) on the responses (y-axis) for dissimilarity to mature forest (Left) and cover of MFI species (right), for three regrowth ages, two rainfall levels, presence or absence of coppice, and two site groups assuming an average slope of 20%, and a pH of 4.75; Predictions based on finite mixture modelling (Appendix 3.2.2: Table 3–C).

3.4.5 What is the estimated depth of mature forest influence (DFI) for species assemblage?

For all three age classes NCAP reached a maximum canonical correlation with a *P*-value of 0.001 using 9999 randomizations, and in all cases provided a better fit than the equivalent linear CAP model regardless of whether the data were square root transformed or not (pseudo F all > 0.55, $P = 0.001$ using 9999 randomizations).The logistic model fit was best for young regrowth stands ($R^2 = 0.95$) and least successful for the later-stage regrowth ($R^2 = 0.63$) with the square root transformed data. For square root transformed data the estimated DFI varied from 17.1 m in young sites to 26.5 m in late-stage sites (Figure 3-8). For untransformed data the range between the youngest and late stage sites was from 16.1 m to 26.0 m. Like the results of PERMANOVA and linear mixed effect modelling, the NCAP results also provide evidence that there is a gradient in species assemblage associated with DFI. Since the mean estimate for the mid and late stage data is beyond the 95% confidence interval of the young stage data the hypothesis that the DFI changes with forest age was partially supported. There was however no evidence that the DFI differed between the mid and late stage sites since the estimates for these differed only by 1.7 m although the confidence interval extended much further into regrowth forest for the late stage sites (Figure 3-8). The omission of plots with coppice increased the estimated DFI by six metres for late-stage sites and two metres for the younger site sets (results not shown). Including coppice plots, but combining the mid and late-stage data, the estimate for DFI was increased to 30 m (95% CI: 15 to 63 m, $F = 0.67$, $R^2 = 0.67$, $P = 0.001$, 10000 randomizations). Using this site set and transforming it to relative cover of the understorey species (i.e. excluding eucalypts) the DFI estimate increased to 40 m although the model fit was poorer (95% CI: 11 to 57 m, $F = 0.46$, $R^2 = 0.62$, $P = 0.001$, 10000 randomizations). When the relative covers of MFI species were analysed without other species, the estimated DFI increased to 48 m (95% CI: 5 to 83 m, $F = 0.52$, $R^2 = 0.53$, $P = 0.001$, 10000 randomizations).

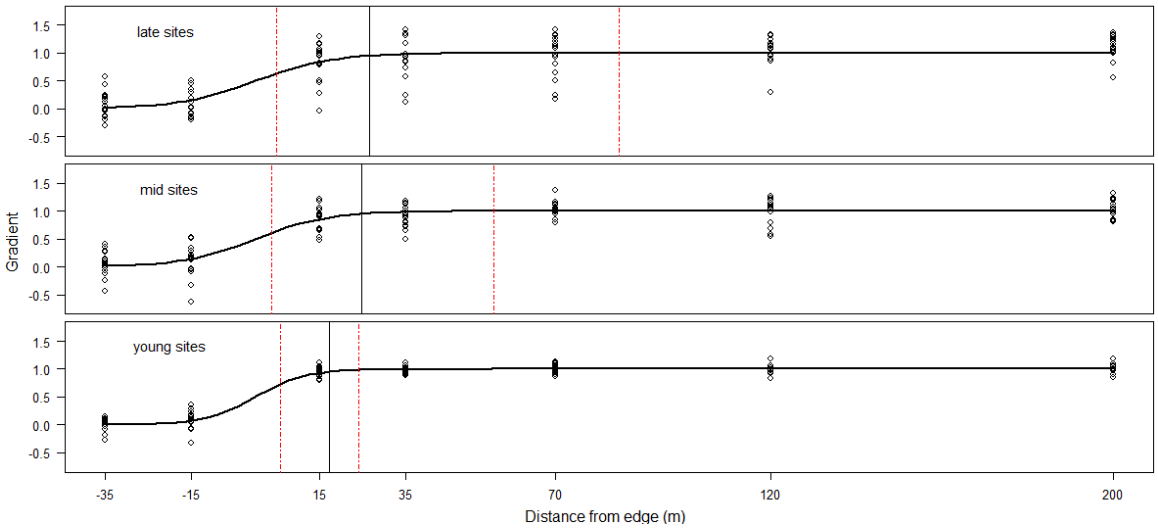


Figure 3-8. Plot of logistic fit for distance gradient for square root transformed plant community data using NCAP marked with estimate of the depth of mature forest influence within regrowth forests (95% dissimilarity to mature forest assemblage) with 95% confidence intervals for each age class (young stage regrowth~7 years: 17 m, CI: 6 to 24 m, $R^2 = 0.95$; mid-stage ~ 27 years, 25 m, CI: 4 to 55 m, $R^2 = 0.78$; and late stage~ 45 years: 26 m CI 5 to 85 m, $R^2 = 0.63$, P all < 0.001 for 10000 randomizations).

3.5 Discussion

3.5.1 Is floristic composition in regrowth forest associated with DMFE?

The results for assemblage variation, species richness and Shannon's diversity index, all provided clear evidence in support of the hypothesis that floristic composition in regrowth forest is associated with DMFE.

This study extends that of Tabor et al. (2007), who found a distance effect for densities in four rainforest tree species, by demonstrating that the response to mature forest influence extends also to richness and cover of mature forest species, total species richness and diversity, and to variation in community assemblages. Baker et al. (2013a) demonstrated that while one year old silvicultural regrowth was quite markedly different in floristic composition with mature forest communities, that the regrowth assemblage nevertheless retained similarities with adjacent vegetation. This

study, extend theirs by providing evidence that the similarity between adjacent communities increase with regrowth age. These results are also consistent with observations of secondary forests elsewhere in the world (Matlack 1991; Grau 2004; Verheyen et al, 2006).

A concurrent study of birds at the same sites used in this study of vascular plant species, was unable to demonstrate mature forest influence on bird assemblages, bird richness or frequency of individual bird species (Hingston et al. 2014). However, they reasoned that the greater mobility of birds resulted in a difference in the scale of response to mature forest by these species in comparison to those less vagile. In support of their hypothesis, a study in the same region demonstrated that bird abundance and assemblage differences were associated with the proportion of mature forest in landscapes measured at scales of more than 500 m radius, and seemed most associated with scales of one to two kilometres (Wardlaw et al. 2012). In a study of fragmentation effects on bird diversity, Tubelis et al. (2007) examined the bird diversity in plots within peninsulas of native forest in a matrix of pine plantation, with plots located from the edge of core native forest up to a distance of 600 m from the boundary with core forest. They found were able to detect a decline in the number of bird species across this scale of 600 m. They also observed that increasing the width of the peninsulas was associated with increased bird diversity (Tubelis et al. 2007). Another recent study of birds in the woodlands of temperate eucalypt woodlands in southeastern Australia determined the aggregated diversity of birds within sites (2 ha), farms (1000 ha) and landscapes (10,000 ha) with increases in the native vegetation cover within the site, farm and landscape respectively (Cunningham et al. 2014). Cunningham et al. (2014) also observed that bird diversity within sites was associated with native vegetation cover in the surrounding landscape. The results of Wardlaw et al. 2012 and Cunningham et al. (2014) suggest that birds my be responding more closely to total abundance of their preferred habitat rather than proximity to a particular patch.

Among the factors that Cunningham et al. (2014) considered might have contributed to spatial variability in bird diversity, were metapopulation functions such as inter-patch population movement, colonization and mortality rates (e.g. source and sink dynamics; see for example Levins 1969; Hanski and Ovaskainen 2000) and other

effects of landscape context. Lindenmayer et al. (2008b) describes in more detail the potential mechanisms by which landscape context can influence patch occupancy including the altered conditions at boundaries due to edge effects on rates of predation and parasitism, climate, etc. However, Cunningham et al. (2014) had no data to demonstrate the operation of metapopulation dynamics within their study region. They suggested that the observed spatial dependence between scales in their nested samples contributed to the findings; for example, sites within the same farm and farms within the same landscape were more likely to share common environmental characteristics and approaches to management.

A distance of 200 m was evidently insufficient to demonstrate the influence of mature forest influence on birds given their mobility. It may be that the distance metric was also a less meaningful metric compared with habitat amount for bird species. Such issues or scale and metric may also be relevant to the responses of vascular plant species, particularly those able to disperse over larger distances (Wardlaw et al. 2012).

3.5.2 Is the floristic association with DMFE driven by both pioneer and rainforest species?

The absence of significant associations between the richness and cover of some species groups with DMFE demonstrated that not all species are contributing to the overall floristic association with DMFE. The hypothesis that it is the rainforest species driving the overall trend rather than pioneer species was only partially supported by the results. The negative association between cover and richness of MFI species and DMFE was the most substantial driver of the floristic association with DMFE, rather than the association between rainforest species more generally. The results suggested a competitive response might exist between MFI species and other pioneer species since the former were negatively associated with DMFE while the latter were negatively associated with DMFE.

3.5.3 Does the strength of association with DMFE vary among plant persistence and dispersal classes?

3.5.3.1 Dispersal trait groups within rainforest species

The variation in seed dispersal ability may drive floristic changes with DMFE (Tabor et al. 2007; Baker et al. 2013b). The hypothesis that there would be variation in responses to distance between rainforest species due to differences in traits was borne out by the absence of an association between DMFE and the soil seed-store species *Acacia melanoxylon*, as well as the observed variation in the steepness of gradients between the other groups of rainforest species.

The strong sensitivity of rainforest ferns, and weaker response of pioneer ferns to isolation from mature forest did not align with the hypothesis that wind dispersed taxa with spores would be less sensitive to isolation from mature forests than species without attributes that aid long distance dispersal. Fern spores are able to disperse over many hundreds of kilometres, yet other studies have also demonstrated a similar pattern of sensitivity to isolation among the Pteridophyta. Tájek et al. (2011) found that islands of serpentine rock habitat which were isolated from others by more than 4 km were less likely to be occupied by one of two rare fern species. Fern richness patterns within fragmented forest patches in Kyoto had a negative association with increased isolation from mountain forest located at distances of up to 3 km away (Murakami et al. (2005). Richard et al. (2000) found that the patterning of fern species richness across a one hectare patch of mature forest in Quebec was explained by environmental variation for data aggregated to scales of 15 m^2 or more and optimized for a 25 m grid. However at smaller grid sizes environmental variation between grid cells was unable to explain fern richness. At smaller grid scales, the effects of contagion appeared more important than environmental differences, with the chances of a fern species establishment being more to do with the abundance of locally produced spores than habitat suitability. Such a 'mass effect' (*sensu* Shmida and Wilson 1985) could well be contributing to the observed reductions in species richness with DMFE for rainforest ferns, since it is likely that there is a substantial reduction in spore availability with increased DMFE, giving rise to a distance effect in

fern richness, despite a very high likelihood that smaller quantities of spores of all the rainforest fern species are capable of dispersing much greater distances than 200 m.

The results of the present study also differed from expectation by demonstrating that rainforest angiosperms with wind-dispersed seed were more strongly associated with DMFE compared with species with heavier fruits distributed by vertebrates. This result is in agreement with frequency differences among species by Tabor et al. (2007). It indicates that the capacity of species to disperse over long distances is not necessarily strongly correlated with the statistical probability that such dispersal events will either occur or be successful. This result may be explained by the fundamental interference of gravity, even for seeds adapted for dispersal by wind. Evidence for exponential decline in seed has been provided for three dominant rainforest tree species in Tasmania, including the wind-dispersed species *Atherosperma moschatum*. Few seeds reached 150 m and the great majority of seeds for all three species studied by Hickey et al. (1983) fell directly below the parent trees. The seeds of *Nothofagus cunninghamii* and *Eucryphia lucida* which reached the greatest distances away from their parents were smaller than average and had a lower germinability (Hickey et al. 1983). Although more *Atherosperma moschatum* seeds may disperse over greater distances, the rate of germination success has been observed to be poorer than for other rainforest tree species (Hickey et al. 1983; Read and Hill 1988). Within mature forest the combination of short average dispersal distances for both pollen and seed in *Atherosperma moschatum* and its habit of vegetative regeneration, has resulted in clumped neighbourhoods of genetically similar and inbred trees (Shapcott 1995). Nevertheless local forest patches often include genetically distinct clumps, while genetic differences between stands were not strongly correlated to distance, demonstrating the capacity for *Atherosperma moschatum* to disperse long distances, at least over long time scales (Shapcott 1994).

Forest studies in other regions have also demonstrated the sensitivity of seed plants to mature forest influence, and have linked this mature forest influence to dispersal capacity as well as other traits. A study of 82 German forest seed plants demonstrated the traits most associated with a negative response to isolation and fragmentation were clonal specialists, insect pollination and a low production of heavy, short-lived diaspores without structures for dispersal (Kolb and Diekman 2005). Verheyen et al.

(2006) demonstrated that species with long distance dispersal traits formed a higher proportion of forest herbs in young secondary forests of Flanders that were isolated from other forest. Matlack (1994) demonstrated average dispersal distance per year varied substantially according to the method of dispersal. In particular he reported that plants with seeds which were ingested by or adhered to vertebrate fauna were able to disperse much farther per year than species dispersed by wind. Wind dispersed plants were observed to have greater rates of expansion into secondary regrowth forests per year than species without any adaptations for dispersal.

In an experimental old field study at one large site in Kansas (USA), Yao et al. (1999) found that distance to adjacent forest affected the density of several woody plant species. Contrary to the results of Matlack (1994) they anticipated that wind dispersed trees would colonize prior to bird dispersed trees but found that these species began colonizing at the same time and concluded that, in situations where the seed source of both is close, the dispersal mechanism plays only a minor role in the speed of establishment and density and that characteristics of growth and competition rapidly become more important in determining success.

In another study of spatial patterns in species composition in abandoned agricultural land, this time in the Argentine subtropics, the proportion of bird-dispersed plants was found to depend on the presence of citrus trees (abandoned citrus orchards) which served as bird perches (Aragón and Morales 2003). Higher proportions of wind-dispersed plants were found dominating the herbaceous cropland areas, while exotic species declined with distance from current agricultural activity (Aragón and Morales 2003). It is clear from these varied studies that there are a multitude of mechanisms which may affect the success of species with DMFE.

3.5.3.2 Dispersal trait groups within pioneer species

Contrary to the hypothesis that none of the dispersal and persistence trait groups would confer a sensitivity to mature forest influence within pioneer species, there was a weak negative association between the linear effect of DMFE and pioneer ferns and a weak linear positive association with distance for species with soil-stored seed. The negative association between the pioneer ferns, which was found only in the youngest

age class, suggests that the closest propagules sources for the pioneer ferns were found within the adjacent mature forest. The absence of a trend in older forest is likely to be because of a reduced abundance of pioneer ferns in the older regrowth forest and the availability of propagules from within the regrowth patch that provided much closer sources of propagules than the adjacent mature forest.

The hypothesis that pioneer species may be affected by competitive exclusion close to the boundary was partially supported only by the weak positive association between pioneer species with soil stored seed and DMFE.

3.5.4 What is the response magnitude of the floristic association with DMFE?

The magnitude of the effect of DMFE on the response variables varied between analytical methods and in association with other environmental variables. Statistical approaches that did not take into account variation due to other environmental differences at each site were able to demonstrate only weak floristic responses due to DMFE. Although PERMANOVA did take into account the random effects of sites it also provided evidence for only a small effect between DMFE and assemblage variation. But the PERMANOVA analysis provided only a comparison of assemblages within each plot with the assemblages of all other regrowth plots. It was not able to directly compare assemblages with the adjacent mature forest assemblages. Nevertheless, these results for a weak effect from DMFE, were in keeping with those from other studies for this region which although not examining the effects of landscape context, they have shown that assemblages are strongly associated with differences in soil fertility, climate and regrowth age (Corbett and Balmer 2001; Doran et al. 2003). These results serve as a reminder that close proximity to mature forest patches does not automatically give rise to wet forest assemblages rich in rainforest species. To this extent the effect of DMFE on floristic variation appears to be small in comparison to the effects of disturbance history, climate and soil type on assemblage variation at regional scales.

In contrast, the results presented from statistical analyses which partitioned variation in responses due to random effects and other environmental differences demonstrated

that the magnitude of DMFE effect on dissimilarity to mature forest and the richness and cover of MFI species can be as important as other environmental variables at the local patch scale. The implication of these results may be important in understanding successional dynamics of these forests and potential for floristic change over longer time-scales. The variation in predicted effect-size demonstrates that there are complex interrelationships between floristic responses, site environment, regrowth age and DMFE. However, before going onto examine the results of the analyses reported here which suggest that there are interactions between age, climate and DMFE on species responses, it is important to note that the number of sites examined in this study was small (15). With such a small sample size there is inevitably a higher risk that the results could include aberrations due to the inclusion of one or two sites with unusual species responses.

While the results presented from both LME and finite mixture models provide evidence in support of the general importance of mature forest influence for recovery of MFI species richness and cover in wet eucalypt forest following harvesting, they also demonstrated situations in which this was not the case. Although some variation in the responses was apparent across the DMFE gradient in young regrowth, this variation was minimal, and the effect magnitude of DMFE therefore generally very small. At young sites climate and topographic position had a much stronger influence on the response variables. Likewise there were site environments in which MFI species recovery is slow after harvesting and at these sites there was also only a minimal effect from DMFE on the responses studied, even at sites with older regrowth (e.g. steep slopes, northerly aspects, low summer rainfall). In late stage regrowth at high rainfall sites with favourable conditions for the re-establishment of MFI species, the cover of MFI species can be very high at the boundary of mature forest and declines relatively slowly with DMFE, demonstrating another situation where the effect magnitude of DMFE is relatively minor. However in the latter example, the potential DFI is likely to be much greater than at other sites.

As in Yellowstone National Park (Turner et al. 1997), vegetative regeneration by rainforest tree species resulted in a more rapid succession to mature forest. Resprouting plants grow more rapidly, and mature and reproduce more quickly, than those colonizing from seed. Where species were are able to recover vegetatively there

was a reduced dependence on mature forest influence for site recovery and the magnitude of the effect from DMFE on the MFI species cover and dissimilarity to mature forest was reduced. Coppice appeared not to affect species richness of MFI species. Despite these results, coppice regeneration of rainforest trees is uncommon following current silvicultural regeneration treatments. Tree ferns are most likely to resprout, although more frequently killed by timber harvest operations than in wildfires (Ough 2001). Coppice regeneration of rainforest trees (excluding tree ferns) was present in only 10% of plots, and was largely restricted to sites which had been old growth forest prior to logging. At the sites measured by Tabor et al. (2007) four percent of the stems counted of the four rainforest trees had originated from resprouting legacy plants. Other studies have also observed a higher rate of recovery by coppice in burnt areas that had not been logged compared with neighbouring areas which had been logged and subject to aggregated retention harvesting and regeneration burning (Baker et al. 2013a). A strong relationship has also been observed between the recovery rates in rainforest species after wildfire and their capacity to regenerate vegetatively which has been linked to fire frequency and severity (Barker 1991; Lawes et al. 2014; Clarke et al. 2015). Although Jordan et al. (1992) did not describe the relative proportion of vegetative recovery compared with seed germination, they demonstrated that the most rapid recovery of rainforest plants in silvicultural regrowth was associated with less severe regeneration burns.

Another aspect of post-fire recovery that is likely to have an interactive effect with proximity to mature forest and vegetation age is that of herbivory (Baker et al. 2013b). Browsing pressure by marsupials is a major barrier to plant establishment in regenerating eucalypt forest (Cremer 1969; Dickinson and Kirkpatrick 1986). Total biomass and species richness is higher in fenced areas compared with unfenced areas of young forests (personal observations, Dickinson and Kirkpatrick 1986). Some studies have demonstrated a decline in browsing activity with increased distance away from forest margins (e.g. Wahungu et al. 1999). In a study of Tasmanian timber plantations, a decline in browsing damage with distance from the edge was observed in one third of plantations studied (Bulinski and McArthur 2000). Varying palatability is likely to contribute to variation in survival rates among species. At least one study in tropical forest has demonstrated that fast-growing pioneer species are characterised

by few defences against browsing (Coley 1983). However, Dickinson and Kirkpatrick (1986) reported that excluding browsers in regenerating dry eucalypt forests increased the growth of woody plants and graminoids at the expense of forbs and grasses. Browsing has been reported as a barrier to the recruitment of several slow growing rainforest canopy trees in Tasmania, including *Atherosperma moschatum* and *Athrotaxis cupressoides* (Cullen and Kirkpatrick 1988; Neyland 1991). Hence, it is not useful to generalise browsing responses in pioneers or mature forest species groups as a whole, and no data on browsing was collected in the current study with which to assess the relative importance of herbivory in the changes in species abundance and assemblage with DMFE or with increasing forest age.

A related question to the one posed about the effect magnitude of DMFE on floristic responses is whether the abundance of MFI species within the adjacent mature forest affects mature forest influence? The sampling design provided only a limited opportunity to test this proposition. Sites were selected only where mature forest patches contained a good cover of rainforest species in the understorey. The variation in MFI species cover in mature forest was strongly associated with rainfall and was highest in old growth patches. However, contrary to expectations dissimilarity to mature forest was positively associated with this predictor. This can only be explained by the much greater differences between regrowth assemblages and assemblages in old growth patches compared with assemblages of regrowth and mature forest patches burnt since 1898. Therefore this result does not provide any evidence that high cover of MFI species in mature forest generates a stronger mature forest influence. However, the reduced response size of MFI species cover in association with DMFE in situations where there was high covers of MFI species in adjacent mature forest may suggest that the DFI is greater in response to higher cover of MFI species. Alternatively it may simply be that there is a difference in the rate of recovery by MFI species at harvested sites which were previously occupied by old growth forest compared with forest burnt since 1989. Unfortunately, the confounding of rainfall, MFI species cover in mature forest plots and coppice regeneration, which was also associated with sites that had been old growth prior to harvesting, prevents a clear interpretation of results.

Fundamental to understanding mature forest influence is the need to distinguish which effects associated with DMFE provide evidence for mature forest influence and which are the result of changing site environments with increased spatial separation. The methods adopted here attempted to ensure that at least some of the environmental variation was accounted for by including environmental covariates in the model. Despite the inclusion of the most highly correlated environmental variables, DMFE was always significantly associated with the response variables, providing support for the assumption that DMFE is providing an indirect measure of mature forest influence. Likewise, when tested, DMFE remained a significant contributor to the explanatory power of response variables even with the inclusion of the environmental dissimilarity variable.

The large between site differences in the responses within the LME models was only partly reduced by including the climate variable rainfall in the warmest quarter in the finite mixture models. The sampling design for this study did not take into account the variation in disturbance history and despite testing the factor for fire frequency, it failed to be included. The confounding between variables for disturbance history, site regrowth age, rainfall, coppice and the variable MFI species cover in mature forest plot are all likely to have contributed to the difficulty in revealing a particular component of the variation which was directly attributable to disturbance history. However, among the sites that were included in the site group with lower richness and cover of MFI species and higher dissimilarities to mature forest, most, although not all, were sites that had been burnt since 1898. It seems quite likely that, although the models have not demonstrated this relationship, sites burnt in 1989 or more recently and then harvested have been much slower to recover in some instances than sites which were old growth prior to harvesting. In addition, it is also possible that broader scale landscape effects such as the abundance of mature forest in the surrounding region may be contributing to additional unexplained variability in some responses, particularly for species with greater dispersal range.

Most importantly for understanding successional dynamics the results demonstrate that succession does not occur homogeneously with forest age but occurs more rapidly close to the mature forest boundary and in response to wetter situations on gentle, south facing slopes. In other words it is rapid in situations where the

establishment and survival of rainforest species is likely to be better. This relationship was also observed in the assemblage data for beetles within the same sites (Fountain-Jones et al. 2015).

3.5.5 What is the estimated depth of mature forest influence for species assemblage?

For both plants and beetles the estimated depth of mature forest influence was smallest in the young-stage regrowth. Recovery of beetle assemblages occurred more quickly than vascular plant assemblage over the 45 year chronosequence. The DFI for beetles was estimated as 176 m in late-stage regrowth (Fountain-Jones et al. 2015) compared with the estimate for plants of between 26 to 48 m depending on whether the data included all species or excluded pioneers. The uncertainty for the depth of mature forest influence estimate was much less for plants than beetles, providing greater confidence that the successional changes within the floristics of wet eucalypt forest are most commonly restricted to the first 50 m from the boundary. Nevertheless, there was a greater variation in the relative cover of mature forest species and in dissimilarity of regrowth to adjacent mature forest with increasing forest age, making the predictions of these responses more difficult in late stage regrowth.

Baker et al. (2013b) were able to demonstrate a change in the assemblage of bryophyte species with DMFE. They report that their results were consistent with a DFI of approximately 50 m although the actual distance at which the assemblages were similar to the adjacent mature forest also had a high degree of uncertainty. They also noted that the depth of mature forest influence was greater for logs than for ground substrates (Baker et al. 2013c). Spores of bryophytes are readily dispersed by wind, so a depth of 50 m for both vascular and non-vascular plants was somewhat surprising. However Baker et al. (2013b) suggest that it is the sensitivity of bryophytes to microclimatic conditions that creates a barrier to colonization further from the mature forest edge. At the same sites for which the vascular plant data is presented here, Baker et al. (2014) have demonstrated that microclimate in the regrowth forest, varies with proximity to mature forest. They showed that at the boundary there were less extreme fluctuations in temperature and low vapour pressure

deficits, and low mean daily temperatures in the warm summer months (Baker et al. 2014). The differences in microclimate between the edge and 200 m away were most pronounced in summer and on hot windy days for the mid-stage regrowth forests, and least pronounced for the youngest stage regrowth. The air within the understorey of mature forest receives less solar radiation and wind by virtue of the density and height of the vegetation, and is thus less prone to extreme fluctuations in temperature or moisture than unforested sites. The mature forest air mass mixes with that of adjacent air mass at the boundary serving to moderated the temperatures and moisture levels in the of air of adjacent regrowth forest. In addition the mature forest shades the adjacent site for at least part of the day and provides shelter from wind. The greater canopy heights of the late-stage regrowth, which were approaching those of the mature forest and the increased density of trees and tree-ferns in these regrowth understoreys, resulted in the reduced importance of mature forest influence on microclimates in late-stage regrowth compared to mid-stage regrowth. Thus, mature forest influence on microclimate would explain the relationship observed between DMFE for well dispersed, but climatically sensitive, species, such as bryophytes and also ferns and other rainforest plants. For example Black (2013) demonstrated that the spatial position of individual tree ferns in relation to DMFE was a strong predictor of epiphytic fern richness at some of the same site used in this study.

The effect of DMFE on fern species richness may also relate to variation in suitable substrate availability. Within logging sites the distribution of suitable substrates may not be independent of DMFE. In particular tree falls of mature eucalypts falling from adjacent mature forest into the site will be located at the mature forest edge. The distribution of logging slash is often concentrated on site edges (personal observation). Mature tree ferns, a favoured site for epiphytic fern establishment, were found to have a negative association with DMFE (data not shown). A reduction in available micro-sites for establishment has been suggested as one of the likely causes for the lower frequency of epiphytic ferns in logged forests than regrowth forests generated by wildfire (Hickey 1994).

3.5.6 Conclusion

There was strong evidence the floristic composition of regrowth forest following timber harvesting is influenced by mature forest proximity, although the response is not uniform. This study established that mature forest influence affects species richness diversity and assemblage variation but may be weakest in sites where conditions are adverse for the establishment of rainforest species. The presence of resprouting plants is associated with much more rapid recovery of mature forest assemblages than recovery from seed. Although the data here suggests that the average DFI is only about 50 m in late stage regrowth it is possible that this will continue to increase as the regrowth forest ages, although there was little difference in estimates for mid and late stage regrowth. The models showed a continuing increase in richness of mature forest species in the regrowth with age, suggesting that new rainforest species are still establishing in the understorey of regrowth forest up to 50 years after disturbance, despite the canopy closure that occurred in the first 20 years

“Single trees are extraordinary; trees in number more extraordinary still. To walk in a wood is to find fault with Socrates's declaration that 'Trees and open country cannot teach me anything, whereas men in town do.' Time is kept and curated and in different ways by trees, and so it is experienced in different ways when one is among them. This discretion of trees, and their patience, are both affecting. It is beyond our capacity to comprehend that the American hardwood forest waited seventy million years for people to come and live in it, though the effort of comprehension is itself worthwhile. It is valuable and disturbing to know that grand oak trees can take three hundred years to grow, three hundred years to live and three hundred years to die. Such knowledge, seriously considered, changes the grain of the mind."

"Thought, like memory, inhabits external things as much as the inner regions of the human brain. When the physical correspondents of thought disappear, then thought, or its possibility, is also lost. When woods and trees are destroyed -- incidentally, deliberately -- imagination and memory go with them. W.H. Auden knew this. 'A culture,' he wrote warningly in 1953, 'is no better than its woods.' ”

Robert Macfarlane, The Old Ways: A Journey on Foot Penguin Books; Reprint edition (2013).

Chapter 4 Species response to landscape context

4.1 Abstract

The relative importance of landscape influence compared with site environment in determining the abundance of common plant species in wet eucalypt forest is tested in this chapter.

PERMANOVA analysis revealed an interactive effect between proximity to mature forest and fire frequency such that regrowth forests burned twice or more had greater assemblage difference with distance from the boundary than plots burnt only once. Mature forest indicator species were more strongly associated with regrowth forest sites close to mature forest edge compared with regrowth forest more distant from it. In most cases the distribution of pioneer species was less strongly affected by proximity to mature forest. Species abundance models developed using a combination of landscape metrics and site parameters as candidate variables performed better than models developed from site variables alone for a majority of species. However, the variance explained by landscape metrics alone was typically lower than that explained by soils, climate, topography and disturbance history. Among the highest ranking landscape metrics were proximity to mature forest and proportion of mature forest in the surrounding landscape. Patch size was found to be a less useful predictor of individual species abundance in regrowth forest. Despite most pioneer species having traits to survive or persist through disturbance or the capacity to disperse over long-distances, many of these species were negatively associated with mature forest metrics, whereas the mature forest species were usually positively associated with these metrics. There was little evidence that the strength of association between plant species and LC metrics was related to their persistence or dispersal traits suggesting that the mechanisms by which the landscape influences plant species abundance and distribution are probably complex and non-linear.

Increased disturbance frequency was associated with a reduced abundance of mature forest species, but this reduction was less in areas close to mature forest demonstrating the proximity to mature forest mitigates against the impact of disturbance. Continued reduction in mature forest habitat could therefore result in a

loss of landscape resilience. This loss may be averted by protecting both remaining mature forest areas and strategically targeted patches of regrowth forest.

4.2 Introduction

Most habitat modelling grounded within ecological niche theory (Hutchinson 1957) relates species response (presence, abundance or reproduction) to gradients in the environment (McCune and Grace 2002; McCune 2011). It is also well established that site history, including disturbance frequency and time since last fire, is important in determining community assemblages and vegetation structure (e.g. Attiwill 1994). However, there is growing empirical evidence, supported by metapopulation theory, that species survival and reproduction is influenced by the surrounding landscape as well as immediate site conditions (Levins 1969; Saunders et al. 1991, 1999).

A problem with some experimental studies of landscape influence for plants can be the delay in responses of long-lived individuals. For example, a fragmentation experiment begun in 1987 in Australian temperate eucalypt forest (Margules 1992) took several decades before changes in vascular plant communities could be detected in the remnant native vegetation (Morgan and Farmilo 2012). Some non-experimental studies have found little or no correlation between landscape patterns (e.g. patch size, isolation etc) and vascular plant species assemblages and/or diversity (e.g. Kirkpatrick and Gilfedder 1995; Woolley and Kirkpatrick 1999). Although Löbel et al. (2006) found an association between landscape context (LC) and non-vascular plant species composition in remnant European grasslands, they observed no correlation with vascular plant species composition. Given natural environmental heterogeneity and stochastic variability in species distribution patterns, finding evidence of LC influence is difficult in both experimentally fragmented habitats as well as in natural landscapes (Morgan and Farmilo 2012). Distinguishing LC influence may also be difficult if there is a lag in species responses. For example, Krauss et al. (2010) observed that species richness of long-lived plants in remnant European grassland is more strongly associated with past landscape patterns than current patterns.

Pioneer species are defined here as those that are generally unable to germinate and/or grow in the shaded understorey of wet eucalypt forest or rainforest in the absence of

recent disturbance and include the dominant eucalypt species. Species able to establish at the site prior to canopy closure may shape vegetation trajectories during their life-spans (Gilbert 1959; Jackson 1968; Connell and Slatyer 1977; Noble and Slatyer 1978; Noble and Slatyer 1980). Species recovering vegetatively or germinating from soil or aerially stored seeds do not rely on long distance dispersal to regenerate at a site after disturbance (Noble and Slatyer 1980). Obligate seed regenerators that lack a canopy or soil seed store are more likely to be most dependent on dispersal from mature populations. Among these plant species it is likely that those less capable of dispersing over long distance will be more sensitive to LC and consequently also to changes in disturbance regime, assuming that there are no other physical or biological barriers to species establishment post-fire, apart from distance to a propagule source (Noble and Slatyer 1980).

Within production forest regions, harvesting of timber and wildfire alters the demographic patterns in forest landscapes. This study addresses several aspects of assemblage and species abundance change in association with time since disturbance and variation in LC by investigating the following related questions:

1. Do assemblages vary with age?
2. What are the indicator species of each successional stage and do they differ in their trait characteristics?
3. What variables are the best predictors of floristic response – LC metrics or site environmental variables? This is analysed for forest assemblages and individual species abundance for several forest age classes and using different statistical methods to test the robustness of the results.
4. Can species traits be used to predict species abundance response to LC?

4.3 Methods

4.3.1 The study area

The study site was an approximately 26 km x 33 km area in the Southern Forests of Tasmania (Figure 4-1). The sample plots were all located within tall wet eucalypt forests *sensu* Kirkpatrick et al. (1988) at altitudes below 600 m and receiving an average of at least 1000 mm rainfall each year. The majority of these forests were

dominated by *Eucalyptus obliqua* and/or *E. regnans*. A more detailed description of the study area was provided in chapter 2.

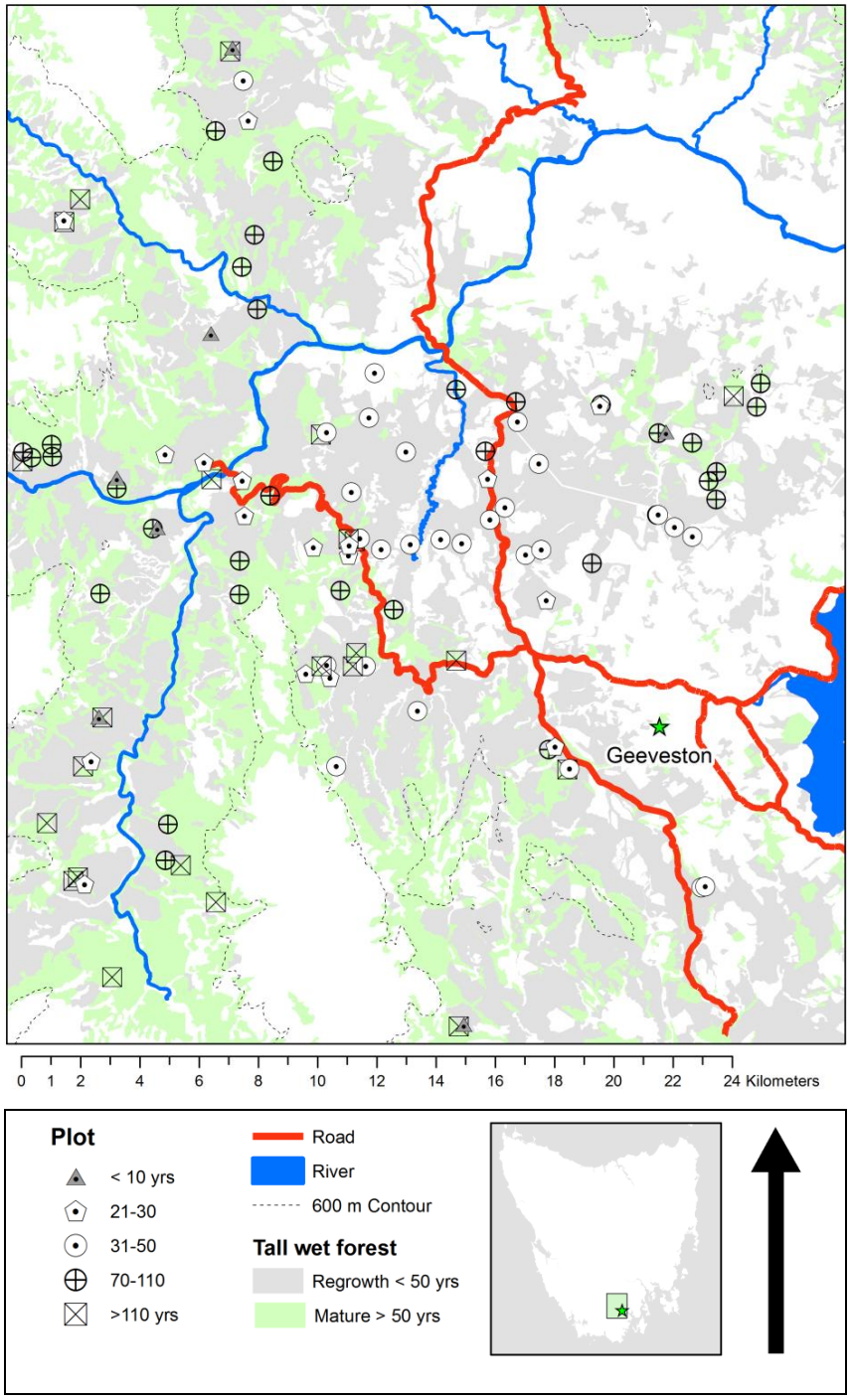


Figure 4-1. Study area in Tasmania, showing location of 107 plots in tall wet forest forests by age class in 2009 and the township of Geeveston (43° 10'22"S, 146 ° 54'28"E)

4.3.1 Forest age terminology

Regrowth eucalypts are defined as trees under 110 years old, while older eucalypts trees are defined as mature trees. 'Regrowth forest' is defined for this chapter as any forest burnt in the last 110 years, regardless of whether the forest retains mature trees (Table 4–1). The term 'old growth' is used here to refer to forest that has not been disturbed by fire or logging for more than 110 years (Table 4–1). ‘Mature forest’ is used to include both old growth forests and those regrowth forests that have not been disturbed for more than 50 years (although most was disturbed prior to 1935) that retain eucalypts that are older than 110 years. The terms ‘regrowth forest’ and ‘mature forest’ are not mutually exclusive (Table 4–1).

Table 4-1. Definition of terms for eucalypt forest age classes and codes#

		Code		Forest classes	Years since disturbance	
Regrowth		SR	YSR	Young silvicultural regrowth *	<20	<50
			Silvicultural regrowth			
			OSR	Older silvicultural regrowth *Δ	20–50	
	Mature		MR	Mature forest with wildfire regrowth^	50–110	>70
			OG	Old growth#	>110	

* The standard silvicultural treatment at most sites involved clear-felling followed by an intense regeneration burn and aerial sowing with eucalypt seed. Some of plots had been selectively logged or burnt in wildfires in the century prior to being clear-felled

Δ Four OSR plots were burnt in wildfires but showed no evidence of having been clear-felled.

^ Seven plots included in the MR plot set had less than 5% mature eucalypt density and some of these and others may have been subject to selective logging as well as wildfire prior to 1950.

Several plots included in this OG plot set had been disturbed naturally by tree falls, some may have been subject to minor selective logging more than 80 years ago have not been burnt by wildfire were not burnt in the last century.

4.3.2 Data collection

4.3.2.1 Survey design

One hundred and seven 50 x 50 m plots were pooled from several research projects to increase statistical power (Figure 4–1, Appendix 4.1). The final collection was

representative of ages, disturbance history and LC patterns of the native eucalypt forests within the study area. In most plots species abundance (projected foliage cover, PFC) was estimated in five 10 x 10 m subplots to the nearest percent, with species covers of less than 1%, assigned the value of 0.5%. It should be noted that there was no expectation that cover estimates would be accurate to the nearest percent. In fact it is likely that covers of species intermediate between 10 and 90% may actually be accurate only to 5 or 10%, but it was decided to use percent cover figures in order that a better estimate of the rank order of species cover be more precisely estimated than could be achieved by assigning species to broader cover classes. The absolute cover of species in a plot was converted to relative cover. In five plots plant cover-abundance was recorded only in four subplots with the fifth being recorded only by presence-absence. A cover for each species recorded in the presence-absence sub-plot was assigned by calculating the mean percentage cover for each species in the four cover sub-plots. Species not present in any other subplot within the plot were assigned a cover of 0.5% a very high proportion of species infrequently represented within 50 x 50 m plots in wet eucalypt forest were observed to have covers of less than 1%. The relative-cover of all species within each subplot was used to calculate the relative cover of each species within the plot.

There were multiple observers, but the author measured half or more of all subplots within each plot. The conversion of data to relative cover further minimised differences in observer bias. Subplots were located randomly subject to the constraint that they did not share a common side and that at least two plot corners (20 x 20 m) were sampled by at least one subplot.

Plot corners were marked and recorded using a hand-held GPS to a precision varying from 2 m (differentially corrected readings) to 15 m. Subplots were located within the plot using a 50 m measuring tape. Grid references for subplot centres were interpolated from plot corner locations.

Geophytes and annuals were excluded from analysis.

4.3.2.2 Environmental site variables and landscape context metrics

A list of the final subset of environmental variables used in the data analyses is presented in Appendix 4.2, together with the data sources and methods used to derive them. The environmental site variables include topographic, climatic, geological substrate, soil and disturbance variables and were chosen as predictors on the basis of selection frequency and ranking within species models developed from the EFL project plots using Random Forests (Wardlaw et al. 2012).

All spatial analyses and extraction of digital data were undertaken in ARCGIS 9.6 or 10.0 (ESRI 2011). Landscape mapping for each plot was produced by extrapolation from forestry PI-types maps produced in 1947, 1985 and 2010. Meta data for the spatial layers used to generate the landscape metrics are in Appendix 2.2 and Appendix 2.3 of chapter 2.

Four types of LC metrics were used to describe the vegetation landscape of the plots: area, proportion, density and proximity (Appendix 4.3). Four spatial scales (landscape buffer areas defined as 250 m, 500 m, 1000 m and 2000 m radial distances from the centre of the plot) were used to calculate the proportional and density metrics. LC metrics codes (Appendix 4.3) are followed with a single letter code to indicate or the scale they were calculated:

- a (adjacent) = 250 m;
- n (near) = 500 m;
- f (far) = 1000 m;
- and r (regional) = 2000 m.

The area metrics (in hectares) of the forest patches in which the plot was located, were defined by forest type/age class for:

- the current landscape year
- the year the plot was burnt, or
- the landscape year prior to when the plot was last disturbed.

The proportion metrics were calculated as the proportion of particular vegetation classes within a fixed radius buffer.

The average density of mature eucalypts within the buffer area was calculated by multiplying each forest density class of eucalypts by the proportion of the buffer area it occupied and dividing the sum of these by the buffer area.

Proximity metrics measure the distance from the plot centre to the nearest patch of vegetation defined for the relevant metric. Only two classes of mature forest were included as proximity metrics. Proximities were analysed as metric distances in metres. However, the resulting coefficients for the models were then multiplied by -1 for the purposes of presentation. In this way species positively associated (+) with proximity metrics are most abundant when close to the mature forest edge and reduce in abundance with distance away from it.

The LC metrics were calculated for two time periods:

- current year landscape (CY): the approximate landscape as it was when the plot was surveyed; and
- landscape following fire (FF): the plot landscape as it was in the years immediately following the last fire/disturbance, or for plots burnt prior to 1947, then the 1947 landscape.

LC metrics were classified as mature forest metrics if they were measures of the proximity or abundance of mature forest in the landscape.

Proximity to mature forest (PM) classes ‘near’ or ‘far’ were assigned to each plot on the basis of the average distance of the plot centre to three forest types (old growth forest in the landscape following fire, mature forest in landscape following fire and old growth forest in the current year landscape). To ensure sufficient replication in the various combinations of factor levels for age, fire frequency and PM the definition of ‘near’ and ‘far’ differed slightly depending on plot age. Plots under 40 years of age were included as ‘near’ if the plot centre was an average distance of less than 110 m from mature forest, while older plots were classified as ‘near if they were less than 135 m from mature forest. Two plots had centres located between 110 and 135 m.

4.3.2.3 Floristic response variables

To reduce the impact of observer differences on plant cover estimates, relative cover was chosen as the response variable. For multivariate data analysis relativising species abundance by site totals is a common method of standardisation (Faith et al. 1987). This standardisation procedure and Bray-Curtis dissimilarity measure were judged by Faith et al. (1987) to be among the most robust and effective methods for measuring compositional dissimilarity.

Relative cover was calculated by dividing the estimated cover of each species by the sum of the cover of all species recorded in the subplot (excluding orchids and other annuals and geophytes). The relative cover of species in presence-absence subplots was estimated by assigning the average PFC estimate for the four other subplots. Species recorded only in the presence-absence subplot were assigned a cover of 0.5%. The relative cover of each species for the plot was calculated by averaging the relative covers of the subplots.

4.3.1 Data analysis

4.3.1.1 Testing assemblage variation

All multivariate data analysis with the exception of indicator species analysis was under taken in Primer 6.0 (Clarke and Gorley 2006). Bray-Curtis dissimilarity matrices for square root transformed data included all species except annuals and geophytes. The assumption of equal dispersion among groups was tested using permutational analysis of multivariate dispersions (Anderson et al. 2008). Site variables explaining the greatest amount of variation in the data set were determined with distance based linear modelling (DistLM) selecting the step-wise option and R-squared as the measure of best fit (Anderson et al. 2008). All site variables selected at the 0.05 level of significance were included as random covariates in permutation based multivariate ANOVA (PERMANOVA, Anderson 2001) except those incorporated in the PERMANOVA model as fixed factors. A PERMANOVA of all 107 plots investigated the fixed effect of forest age (four classes) and random effects of 12 covariates. A PERMANOVA for data from 84 regrowth forest plots was used to

investigate the three-way fixed effect of age, fire frequency and proximity to mature forest, taking into account the random effects of eight covariates. The permutation tests of significance were based on 9,999 unrestricted permutations of the raw data.

4.3.1.2 Testing of indicator species

Indicator species analysis (Dufrene and Legendre 1997) was undertaken using PC-ORD version 6.08 (McCune and Mefford 2011) to identify species associated strongly with particular age and proximity classes. The complete data set (n = 107) was run four times, with plots allocated into different age group divisions in order to determine which species characterised different successional stages (Appendix 4.4). Species were accepted as indicators of particular forest age classes if the *P*-value for the association was less than 0.1. For all other indicator species analyses the accepted level of significance was a *P*-value of less than 0.05.

Chi-square tests were used to test the null hypothesis that trait groups were equally represented among age-class indicators. Species were assigned to classes of:

- life form (pteridophytes/woody sporophytes/herbaceous sporophytes);
- resprout capacity (known resprouter /rarely or not known to resprout);
- regeneration (continuous / stochastic);
- seed persistence (bradyspore / soil seed bank / fire sensitive); and
- dispersal range (long, medium and short).

Matlack (1994a) provided a generalised ranking of migration rates for forest herbs and shrubs based on dispersal mode: ingested >>adhesive >>wind>>ants>>none. For this study, because of the limited number of species, dispersal range was assigned based on a combination of life-form and dispersal modes. For all life-forms except ferns, ingested seeds and adhesive seeds were grouped with the light plumose seeds dispersed by wind and allocated to the long dispersal range group. Pteridophytes were analysed as a separate class and assumed to have a medium dispersal range due to their minute, wind-dispersed spores. The bradyspores were assumed to include mainly species with fine wind dispersed seed with a medium dispersal range capacity. Species with larger, heavier winged seeds and species with other mechanisms of

dispersal (elaiosomes for ant dispersal, floating seed for water dispersal) or no specialised dispersal mechanism were all allocated to the short range dispersal group.

4.3.1.3 What variables are the best predictors of species abundance

Random Forests modelling

Several methods were used to assess the relative value of using LC metrics compared with site variables for predicting species relative abundance. The first of these involved the use of Random Forests procedure recommended by Cutler et al. (2007) as among the best classification methods available. Random Forests (Breiman 2001) was developed from machine-learning. It is suitable for large data sets and does not assume normality or linear relationships in or between the variables. Random Forest version 4-6.7 (Breiman and Cutler 2012) was used within the statistical software package R (R Development Core Team 2013) with default options (2000 trees, and randomly selecting m predictor variables at each tree node, where 'm' was the integer closest to the square root of the total number of predictor variables**).** For each response variable, an initial model was created to rank all candidate variables. The analysis was run again 10 times, sequentially removing variables in order of least importance. The optimal number of variables to retain in the model was determined as the number with the maximum average explained variance across the ten runs. The analysis was then rerun again ten times, sequentially removing variables until the optimal number of variables remained from which were tabulated three outputs: (1) average rank, (2) importance value (Gini-index) for the top six ranking predictor variables and (3) the average pseudo-R squared (p-R^2).

Meta analysis of Random forest modelling results

Friedman's test was used to compare the relative success of the first series of Random Forests models (R1) developed from five sets of candidate inputs (treatments):

- Site variables only (S),
- Current Year landscape metrics only (CY),
- Current Year landscape metrics and Site variables (CYS),
- Landscape year Following Fire metrics only (FF), and

- Landscape year Following Fire metrics and Site variables (FFS).

The same 42 site variables (Appendix 4.2, R1) were included in all three candidate sets that included site variables. Likewise, the same set of 47 LC metrics was used for all sets including LC metrics (Appendix 4.3, 14 different metrics, of which 11 were calculated for four different spatial scales). The candidate sets including LC metrics were either derived from landscapes following fire (FF/FFS treatments) or the current year landscapes (CY/CYS treatments). Individual species were treated as blocks in Friedman's test but only species for which the modelling was successful ($p\text{-}R^2 > 0.1$) for at least one treatment were included, while species models for which the $p\text{-}R^2$ were negative were converted to 0 prior to analysis. The R1 analysis method was applied to different subsets of the plots, grouped according to age. To determine which subset of plots produced models with the greatest explanatory power the results of the best model from among each of the five candidate sets for each plot set were compared including only species for which all plot sets had produced at least one successful model ($p\text{-}R^2 > 0.1$).

For the older silvicultural regrowth forest plot sets and the set of all regrowth age plots, the difference in $p\text{-}R^2$ for best model including LC metrics was compared with models developed from site variable only sets to determine the extent to which LC metrics assisted in explaining species abundance in this forest age class, and whether this varied depending on species preferred habitat, regeneration and dispersal modes.

To compare models across species a second Random forest analyses series (R2) was undertaken using a single candidate set that included 36 LC metrics from both current and landscapes following fire but calculated at only two spatial scales (500 m and 1000 m) as well as 23 site variables (Appendix 4.2, Appendix 4.3, R2).

To describe which, if any, LC metrics were associated with the abundance of individual species within mature forest, a list of the highest ranking mature forest metric, other vegetation metric and site variable from the best model (highest $p\text{-}R^2$) among two R1 candidate sets tested (CYS and FYS), no meta analyses of these results was undertaken.

Beta regression modelling

Beta regression was developed by Ferrari and Cribari-Neto (2004) to model continuous variates such as proportions and rates which are naturally heteroscedastic and asymmetric. The technique has been further modified by Simas et al. (2010) to handle variable dispersion. Its principal assumption is that the response variable has a beta-distribution. The beta distribution is highly flexible being able to vary in shape in response to two parameters that index the distribution, subject to the restriction of a unit interval (0 to1). Beta regression estimates the mean of the response and the coefficients of linear predictors through a set of regressors and a link function using likelihood based inferential procedures (Cribari-Neto and Zeileis 2010). A major difference from generalized linear modelling (GLM) is that in addition to the regression equation generated for the mean response, there is a separate equation which models the precision of the mean response estimate in relation to another set of predictors. When coefficients of the precision model are significant, this is evidence of unequal dispersion, justifying the use of this technique in preference to GLM.

Beta regression analysis was undertaken using the betareg package (Zeileis et al. 2013) in the R system for statistical computing (R Development Core Team 2013). All regrowth plots were included but old growth plots were excluded in these analyses because the primary focus was to find out how retained patches of mature forest in the landscape influence species recovery within regenerating forest. Because of the time involved in developing models for each species, the set of predictors was restricted to mature forest LC metrics calculated at the 500 m scale from both of current year and landscapes following fire as well as including the distance to mature forest metrics and a range of site variables (Appendix 4.2 and Appendix 4.3).

The most frequently selected and highest ranking predictors from the Random Forest output were used as the input to a step-wise regression for each species. The beta-regression model process was commenced by first fitting the mean, without predictors (null model: y~1) to ensure that the addition of predictors improved the mean estimate. Models were then fitted using the most promising of the climate, soil, topographic, disturbance and mature forest predictors. In the first iteration of modelling, predictors were only fitted in the mean regression model. Predictors that

were not significant in explaining the species response ($P < 0.05$) in the first iteration were then included in the precision equation to determine if this enabled them to fit in the main model. Non-significant variables ($P < 0.05$) were removed first from the precision model and then from the main model one at a time in decreasing order of *P*-value and replaced with alternative but related variables. Categorical factors, such as age, fire frequency and proximity to mature forest were also individually tested in each species model to determine if they improved the model fit. Predictors were added and removed from the model until all predictors included were significant ($P < 0.05$) in explaining variation in species response. Predictors were only included in the precision model when they also occurred within the main model. No attempt was made to fit interactions between predictor variables. In some instances models failed to converge. Alternative models with different predictor combinations were compared using the model Akaike information criterion (AIC) score. Models with the lowest AIC were selected by preference as long as the log ratio test provided evidence that the improvement in the model was significant and the p-R^2 was at least 0.1.

4.3.1.4 Testing association of traits and responses to landscape context metrics

A crude index (0-1), referred to here as the LC Random forest index (LCrI), used the p-R^2 of the best of the Landscape only, site only and combined models to gauge to what extent Landscape metrics explained the variance in species abundance over and above the contribution made by site variables:

IF S > F and L LCr index= 0
IF L>S and F>L LCr index= [(F-L)/2+(L-S)]/T
IF L>S and L>F LCr index= (L-S)/T
otherwise LCr index = (F-[MAX(S:L)]/2) /T
where T is p-R2 for best model
and F, S and L are the p-R^2 scores for models with
F: both LC metrics and site variables
S: site variables only
L: LC metrics only.

The LCrI score was adjusted by multiplying it by -1 (species negatively associated with mature forest metrics or positively associated with other LC metrics) or +1 (species positively associated with mature forest metrics or negatively associated with other LC metrics).

The importance value for mature forest metrics (IVMA) score was calculated by taking the importance value of the highest ranking LC mature forest metric (measured using the Gini index) in the Random Forest model for each species and multiplying it by -1 or +1 depending on the relationship of the species to mature forest metrics (as for LCrI).

The Kruskal-Wallis test was used to test the null hypothesis that the median LCrI and IVMA scores were the same among each species group. In particular median scores for a subset of indicator species of old growth, mature and older regrowth forests which were considered to be fire sensitive were compared with the median scores for silvicultural indicator species. The mature forest indicator species assigned to this fire sensitive group were those which had no effective means of persisting through disturbance and which had only a short range dispersal capacity. Species were included in the tested groups only when their models achieved a p-R^2 > 0.26 for older silvicultural regrowth plots (i.e. n = 44, P <0.01) or greater than 0.18 for all regrowth forest plots (i.e. n = 84, P < 0.10).

4.4 Results

4.4.1 Do assemblages vary with age?

The results of the PERMANOVA (Appendix 4.5) provided evidence that the fixed factor for forest age together with 11 random site covariates were all significant in explaining variation in species assemblages. Age and fire frequency explained similar amounts of the variance (square root of the estimate 15.96 and 15.40 respectively) while soil calcium, soil nitrogen and precipitation in the driest period were the next most important variables (square root of the estimate just over 10).

Table 4-2. Pairwise comparison of assemblages and dispersions within and between age classes.

	Between group similarity#			Deviation from centroid	
Groups		**t-value**	***P*-value**	**t-value**	***P*-value**
OG :YSR	25.9	4.4	0.000	3.36	0.004
OG :OSR	25.6	4.1	0.001	4.18	0.000
OG :MR	35.5	3.0	0.001	3.13	0.005
OSR :YSR	34.0	2.0	0.000	0.30	0.765
OSR :MR	34.8	3.0	n.s.	0.83	0.708
YSR :MR	32.0	2.2	0.000	0.84	0.428
	Within group similarity#			Within group Dispersion	
OG (>110 years, n=23)	52.0			33.0 ±2.1	
MR (70–110 years, n=34)	37.7			43.8 ±1.6	
OSR (40–49 years, n=26)	38.7			42.7 ±2.3	
YSR (0–39 years, n=24)	39.8			41.8 ±1.6	

Note: *P*- value based on permutations, and are rounded to 3 decimal places.

With one exception, assemblages differed between all age class pairs. The exception was that silvicultural regrowth aged between 40 and 49 did not differ from regrowth plots more than 70 years in age (Appendix 4.5). The null hypothesis of equal dispersion between four age classes was rejected (F = 6.3137, *DFI*:3, *DF2*:103, P = 0.002). Old growth forest plots had least dispersion (greatest homogeneity), significantly lower than the younger age classes (P all ≤ 0.005). Dispersion among regrowth forests age classes was least for the youngest class and greatest for the oldest class but the observed differences were not large enough to be distinguishable from chance variation (Table 4–2).

4.4.1 What are the indicator species of each successional stage and do they differ in their trait characteristics?

One hundred and thirty vascular plant species were recorded, of which 70 were in at least 10% of plots within at least one of three age groups: silvicultural regrowth, forest with mature and regrowth trees, and old growth forest (Table 4–3). There were 15 indicators of the youngest age group (< 10 years) but most were species absent in older plots and excluded from the list of 70 species selected for univariate analysis. Among these 70 species, 21 were indicators of old growth forests and 19 were indicators of silvicultural regrowth forest. Six plants were common to all plots with mature trees while another six were indicators only of older regrowth forest.

Species that were indicators of any forest class greater than 50 years in age are from this point forward referred to more generally as Mature Forest Indicator (MFI) species. Species that were indicators of forest classes less than 50 years in age are referred to as Silvicultural Forest Indicators (SI) species.

Pteridophytes were more frequent among old growth indicators than the silvicultural regrowth indicators (ten compared with two including epiphytic ferns, *Chi-Sq* = 5.33, *DF* = 1, *P* = 0.02), while the reverse was true of herbs and graminoids (none among old growth indicators compared with five silvicultural forest indicators, *Chi-Sq* = 5.0, *DF* = 1, *P* = 0.025). Woody plants were equally common in both groups.

The frequency of spermatophyte species with particular dispersal traits did not differ substantially between old growth and silvicultural indicator groups, since both had approximately equal numbers of species transported by birds, wind, or had no obvious dispersal mechanism. However, among the species of silvicultural regrowth indicators was one plant with elaiosomes to attract ants, one with hairs to catch on mammals and another with seeds that float in water, all of which were absent from indicators of old growth forest.

Table 4-3. Summary of traits, indicator value and frequency data for most common species.

Notes and definitions of fields abbreviations & codes

LF– Life forms: C woody climber; G graminoid; S shrub; H forb; E epiphytic fern; F ground fern; T tree;

DT– Dispersal mode: B: ingested, H: hooked appendages, L: small light seeds or spores, P: plumose seed, A: elaiosome, N: none, W: winged pod or seed, O: floats,

S–Seed persistence traits: S: soil stored seed banks, C: bradyspory, K: fire sensitive;

R–Resprouter: R: resprouts after mild disturbance

AC–Forest age class species most associated with species is listed followed by Indicator Value (IV);

Fire freq Cl: Fire frequency class (1 or 2 per century) most associated with species is listed followed by IV information in brackets. Results displayed only for species with IV ≥ 25 and $P \leq 0.05$.

PM x FF Cl: Proximity to mature forest by Fire frequency class most associated with species is listed followed by IV information in brackets. Four classes: N1 = PM Near x 1 fire, N2 = PM Near x 2 fires; F1 = PM Far x 1 fire, PM Far x 2 fires. Results displayed only for species with IV ≥ 25 and $P \leq 0.05$.

PM x 2 Cl: Proximity to mature forest class most associated with species for plots burnt in two or more fires in the last century (plots burnt only once were excluded from analysis), followed by IV information in brackets. Classes: N = PM Near; F1 = PM Far; Results displayed only for species with IV ≥ 25 and $P \leq 0.05$.

IV–Indicator Value for forest age class (IV from the indicator species analysis for which species had the lowest recorded *P*-value).
P-value class is listed in superscript:
n = not significant, # $0.1 < P < 0.05$, * $0.05 < P < 0.01$, ** $P < 0.01$.
The number of classes in the indicator species analysis with best result (Appendix 4.4 for class definitions);

IV of LC metrics in best Random forest model– Provides the importance value (Gini Index) for highest ranking metric. Only values for models with a p-$R^2 > 0.18$ (all regrowth plots) or p-$R^2 > 0.26$ (OSR).

OSR plots: Older silvicultural regrowth plots (between 30 and 50 years since burnt)

All regrowth plots – forest plots last burnt between 0 and 110 years since burnt

Mat LC – Landscape context metrics measuring mature forest

Oth LC – Landscape context metrics measuring abundance of other vegetation classes

OSR: importance score for LC metrics in best Random Forest model produced.

Frequency (%): within three forest age classes in years since disturbance SR (<50) MR (70–110) OG (>110);

Mean Relative Cover: within three forest age classes in years since disturbance SR (<50) MR (70–110) OG (>110).

Species names with an asterisk are those for which the absence of flowers has led to reduced confidence in the identification at species level and nomenclature follows the broader definitions of the species name as described by Curtis and Morris (1975). Unidentified immature plants of *Senecio* (Asteraceae) were grouped with *Senecio minimus*.

Table 4–3				Indicator Species Analysis results				LC metric IV in best Random Forest model				Mat LC in	Frequency (%)			Mean Relative Cover		
	LF	DT	S/R	Age Class	Fire freq	PM x FF	PM x 2	OSR plots		All regrowth		Beta reg	SR	MR	OG	SR	MR	OG
Species name				in years (IV)	CI (IV)	CI (IV)	CI (IV)	Mat LC	Oth LC	Mat LC	Oth LC	Mat	n=50	n=34	n=23	n=50	n=34	n=23
Silviculture indicators																		
Gahnia grandis	G	B	SR	<10 (61 **5)				0	0	0	0	+M	88	82	57	10.0	2.2	0.8
Acaena novae-zelandiae	H	H	S	<10 (26 **5)									10	0	4	0.1	0	p
Pimelea cinerea	S	B	K	<10 (19 #5)				0	0			-M	18	21	13	0.1	p	p
Pimelea drupacea	S*	B	K	20-29 (27 #5)				0	+10	+14	0		82	76	57	0.3	0.3	0.2
Histiopteris incisa	F*	L	R	<40 (41 #4)									64	65	48	1.3	0.4	0.2
Monotoca glauca	T*	B	S	<40 (38 *4)				0	+15	-22	0	0	76	59	52	5.7	3.0	0.4
Leptecophylla juniperina	S*	B	K	<40 (30 **4)	1 (31**)			+11	0	-+21	+6		26	15	39	0.1	0.1	0.1
Eucalyptus delegatensis	T	L	CR	<40 (25 **4)				+16	-13	+14	-11	+M	20	3	0	0.7	0.1	0
*Billardiera longiflora**	C	B	S	<40 (23 **4)						+18	0		16	3	0	0.1	p	0
Senecio species	H	P	K	<40 (22 **4)						-12	+-16		20	6	13	0.1	p	p
Acacia verticillata	T	A	S	<40 (22 *4)						+21	0	+M	30	26	0	1.2	0.4	0
Hypolepis rugosula	F	L	R	<40 (16 #4)				+16	+10				22	18	17	0.1	p	p
Leptospermum lanigerum	T	L	CR	<40 (13 #4)									8	12	0	0.1	0.1	0
Pomaderris apetala	T	N	SR	40-49 (39 **4)	2 (49**)	N2(31 *)		0	0	0	0	+M	58	47	26	22.4	9.6	0.7
Acacia dealbata	T	W	S	40-49 (32 *4)	2 (58**)	N2(35 **)		0	0	+/-21	0	+M	72	41	22	2.3	0.9	0.2
Lepidosperma ensiforme	G	B	S	40-49 (12 #4)				+24	0				10	6	0	0.1	p	0
Eucalyptus obliqua	T	L	CR	<50 (55 **2)				-9	+-12	0	0	0	92	76	74	17.8	14.9	8.0
Zieria arborescens	T	N	S	<50 (19 #2)	2 (33**)			0	+16	0	+16	-M	28	21	0	0.3	0.2	0
Hydrocotyle hirta	H	O	S	<50 (18 *2)									24	9	0	0.1	p	0
Other pioneers																		
*Clematis aristata**	C	P	R	40-49 (15 n4)				+10	-14	0	+21		40	41	35	0.1	0.1	0.1
Prostanthera lasianthos	S	N	S	40-49 (05 n4)									8	8	1	0.2	0.1	0.1
Coprosma quadrifida	S	B	R	40-49 (32 n5)									46	85	52	0.7	0.5	0.1
Pteridium esculentum	F	L	R	<50 (44 n2)	2 (56**)	F2(45**)	F(66**)			-17	0		78	47	17	2.2	2.7	p
Nematolepis squamea	T	N	S	<50 (36 n2)				-13	0	0	0	0	56	56	39	6.7	5.8	0.7

Table 4–3				Indicator Species Analysis results				LC metric IV in best Random Forest model				Mat LC in	Frequency (%)			Mean Relative Cover		
	LF	DT	S/R	Age Class	Fire freq	PM x FF	PM x 2	OSR plots		All regrowth		Beta reg	SR	MR	OG	SR	MR	OG
Species name				in years (IV)	CI (IV)	CI (IV)	CI (IV)	Mat LC	Oth LC	Mat LC	Oth LC	Mat	n=50	n=34	n=23	n=50	n=34	n=23
Eucalyptus regnans	T	L	CR	<50 (31 n2)				0	-20	0	0	0	54	56	26	6.2	6.4	1.7
Dianella tasmanica	G	B	K	<50 (09 n2)				0	0	-13	+13	-M	12	12	0	p	p	0
Bauera rubioides	S	A	S	70-110 (10 n3)									8	15	0	0.4	1.0	0
Correa lawrenceana	S	N	S	70-110 (07 n3)				0	0				10	12	0	0.2	0.3	0
Leptospermum scoparium	T	L	C	70-110 (12 n3)		F2(26*)	F(45*)	-15	0				26	18	4	0.2	0.5	p
Melaleuca squarrosa	T	L	C	70-110 (10 n3)				0	+17	+19	0	+M	16	12	4	0.1	0.5	p
Cyathodes glauca	S	B	K	>70 (36 n2)	1 (40*)			+/-18	-12				46	47	43	0.4	1.8	0.7
Older regrowth/ mature forest indicators																		
Olearia argophylla	T	P	R	70-110 (42 **4)				+-31	0	0	-20	0	42	74	22	1.9	6.7	1.5
Dicksonia antarctica	F	L	R	70-110 (40 *4)			N(68**)	+18	0	+15	0	+M	74	91	65	2.8	7.0	3.5
Polystichum proliferum	F	L	R	70-110 (33 #3)						+17	0		40	62	26	0.5	0.9	0.3
Tasmannia lanceolata	T	B	RS	70-110 (32 *3)		N2(35**)	N(76**)			0	+41	+M	38	62	35	0.2	0.3	0.1
Hymenophyllum flabellatum	E	L	K	70-110 (24 *4)	1 (36*)		N(34*)	+15	0	+23	-18	+-M	26	62	43	0.1	0.2	0.2
Ctenopteris heterophylla	E	L	K	70-110 (22 *4)			N(29*)	+17	0	+13	0		14	41	13	p	0.1	p
Pittosporum bicolor	T	B	R	>70 (38 *2)			N(40**)	+13	-12	0	+38	+M	28	56	57	0.3	0.8	0.5
Asplenium appendiculatum	E	L	K	>70 (17 *4)						+20	0		6	18	26	p	p	0.1
Crepidomanes venosum	E	L	K	>70 (16 **2)									0	18	13	0	p	p
Uncinia tenella	G	H	K	>70 (15 *2)									2	18	13	p	0.1	p
Orites diversifolius	S	W	K	>70 (10 #2)									2	6	17	p	0.1	0.1
Gaultheria hispida	S	B	K	>70 (12 #2)									4	15	17	0.4	0.2	0.0
Old growth forest indicators																		
Anodopetalum biglandulosum	T	W	R	>110 (75 **4)	1 (37**)	N1(40 **)		+30	0	+38	0	+M	20	29	91	1.1	2.3	20.9
Blechnum wattsii	F	L	R	>110 (64 **4)	1 (53**)		N(72**)					+M	58	85	100	0.6	1.3	4.4
Eucryphia lucida	T	N	R	>110 (62 **4)	1 (49**)	N1(43 **)		+28	0	0	0	0	36	38	83	1.7	1.7	15.3
Cenarrhenes nitida	T	B	K	>110 (54 **4)		N1(30 **)							18	21	65	0.1	0.2	1.9

Table 4–3				Indicator Species Analysis results				LC metric IV in best Random Forest model				Mat LC in	Frequency (%)			Mean Relative Cover		
	LF	DT	S/R	Age Class	Fire freq	PM x FF	PM x 2	OSR plots		All regrowth		Beta reg	SR	MR	OG	SR	MR	OG
Species name				in years (IV)	CI (IV)	CI (IV)	CI (IV)	Mat LC	Oth LC	Mat LC	Oth LC	Mat	n=50	n=34	n=23	n=50	n=34	n=23
Atherosperma moschatum	T	P	R	>110 (51 **4)	1 (51**)	N1(36**)	N(76**)	+21	0	0	0	+M	42	74	96	1.1	9.7	13.3
Anopterus glandulosus	T	W	R	>110 (49 **4)	1 (39**)	N1(26 *)		+12	0	+34	0	+M	30	47	83	0.7	0.7	3.0
Nothofagus cunninghamii	T	N	R	>110 (47 **4)	1 (62**)	N1(45 **)	N(73**)	+20	0	+16	0	+M	52	65	96	2.5	8.9	13.6
Hymenophyllum rarum	E	L	K	>110 (46 **4)	1 (46*)		N(46**)	+13	-20	0	-17	0	44	79	100	0.1	0.3	0.5
Hymenophyllum australe	E	L	K	>110 (43 **4)	1 (27**)			+14	0	+20	0	+-M	14	26	65	p	p	0.2
Grammitis billardierei	E	L	K	>110 (43 **4)	1 (50**)		N(45**)	+15	0	0	0	+M	50	82	100	0.2	0.3	0.5
Phyllocladus aspleniifolius	T	B	S	>110 (38 *4)	1 (49**)	N1(36 **)	N(47**)			+19	0	+M	46	50	87	0.9	1.3	2.4
Rumohra adiantiformis	E	L	K	>110 (32 **4)				0	+20	-18	0	0	42	62	83	0.1	0.2	0.3
Sticherus lobatus	F	L	K	>110 (29 **4)									6	3	30	p	p	0.6
Prionotes cerinthoides	C	N	K	>110 (29 **4)									4	6	30	p	p	0.6
Tmesipteris obliqua	E	L	K	>110 (28 **4)			N(40**)	+31	0	+14	0	+M	12	47	65	p	0.1	0.1
Microsorum pustulatum	E	L	K	>110 (28 **4)									26	35	61	0.1	0.1	0.2
Hymenophyllum peltatum	E	L	K	>110 (28 *4)				+11	0	0	0	+M	38	62	74	0.1	0.2	0.2
Aristotelia peduncularis	S	B	R	>110 (25 *4)	1 (34**)							0	20	47	61	p	0.1	0.1
Grammitis magellanica	E	L	K	>110 (22 *4)									6	12	35	p	p	0.1
Olearia persoonioides	S	P	K	>110 (13 *4)									0	0	13	0	0	p
Trochocarpa cunninghamii	S	B	K	>110 (16 #3)						0	0		10	12	26	0.1	0.1	0.4
Other Mature forest species																		
Hymenophyllum cupressiforme	E	L	K	40-49 (15 n4)			N(45**)	+23	+35	+22	+-20		20	29	30	0.1	0.1	0.1
Notelaea ligustrina	T	B	R	<50 (13 n2)			N(25*)						14	3	9	0.2	p	p
Acacia melanoxylon	T	BA	S	70-110 (29 n5)						+17	+-27		54	53	39	1.1	1.8	0.4
Drymophila cyanocarpa	G	B	K	>70 (24 n2)			F(41*)	-28	0	+28	0	+M	38	44	48	0.1	0.1	0.1
Blechnum nudum	F	L	K	>70 (09 n2)						-/+39	0		10	12	13	0.1	0.5	0.1
Coprosma nitida	S	B	R	>70 (07 n2)			N(26*)			0	-24		10	12	13	p	p	p
Trochocarpa gunnii	S	B	K	>110 (11 n3)				0	0	0	0		10	9	17	0.1	0.1	0.2

Among the plant species with mechanisms enabling their seed to persist through disturbance such as bradyspores or species with soil seed-banks, all but two were silvicultural regrowth indicators and only one was an old growth indicator (*Chi-Sq* = 7.36, *DF* = 1, *P* = 0.007).

The 21 old growth indicator species were all species capable of regenerating in the absence of catastrophic disturbance within relatively undisturbed rainforest habitats, while only five species included among the indicators of silvicultural regrowth plots were considered by Jarman *et al.* (1984) to be such species (*Chi-Sq* = 11.56, *DF* = 1, *P* = 0.0007). Resprouting capacity was more difficult to assess since while many species are capable of resprouting after mild disturbance most are killed with more intense fire or when subject to logging followed by burning. However, of those reported to have the capacity to resprout from disturbance there was no difference in their frequency of occurrence in each the two main indicator classes.

4.4.2 What variables best predict floristic response?

Assemblages of all forest ages

The disturbance history and site variables explaining the greatest amount of variation within the 107 plot multivariate data set (in order of significance) were forest age, soil nitrogen, precipitation in the driest period, soil calcium, fire frequency, northwestness, topographic index, soil pH, soil drainage, temperature seasonality and soil aluminium (Distlm, step-wise regression: *Pseudo-F* all ≥ 1.95, *P* all ≤ 0.05, *DF*: 94–105). Together these variables explained 46% of the variance in the data set.

When the near scale LC proportion metrics, current year proximity and current patch metrics were included among those tested, the explanation of the regression model rose to 52% (Distlm, step-wise regression: *Pseudo-F* all ≥1.88, *P* all ≤0.05, *DF*: 89–105). The same site variables remained important in the model with the exception that maximum temperature and soil potassium were included among the site variables while soil aluminium was not.

The LC metrics were less important than most of the site variables. Only proportion LC metrics achieved statistical significance at the alpha level 0.05. Those included

were the proportion metrics for current year landscapes: 40–59 year old forest and 60–109 year old forest; and proportion metrics for landscapes following fire: all non-forest; mature forest including rainforest and 60–109 year old forest. None of the patch or proximity metrics achieved statistical significance at the alpha level of 0.05.

Assemblages of all regrowth forest ages

The site variables that best explained variation in species composition among regrowth plots were calcium, fire frequency, nitrogen, age, precipitation of the driest quarter, maximum temperature, pH, potassium, topographic index, and northwestness (Distlm, step-wise regression: *Pseudo-F* all ≥ 1.99, *P* all ≤ 0.05, *DF* = 73–82), which together explained 42% of the variance.

When LC variables were included (including patch area variables, but leaving site variables unchanged), the variance explained rose to 48%. However, the only LC metrics that improved model strength were those LC metrics that were calculated for landscapes following fire: proximity to mature forest, the proportion of agriculture and plantation areas, and proportion of forest 60–109 years old (Distlm, step-wise regression: *Pseudo-F* all ≥ 1.83, *P* all ≤ 0.05, *DF* = 69–82).

Species composition was associated with the independent effects of the fixed factors age and fire frequency, the interactive effects of fire frequency and proximity to mature forest and the interactive effects of fire frequency and age (Table 4–4).

The species composition in the youngest plots (< 40 years old) differed significantly from those of both the 40 to 49 year old plots and the 70 to 110 year old plots (*P* = 0.05), but the differences between composition of the two older forests did not achieve the 0.05 alpha level of significance.

Fire frequency was associated with significant differences in species composition (t = 2.351, DF = 64, *P* = 0.0001). Among the species that were indicators of forest burnt only once were 11 indicators of old growth forest. Species that were indicators of forests burned more than once included silvicultural indicators *Pomaderris apetala*, *Zieria arborescens* and *Acacia dealbata* (Table 4–3). This group also included *Pteridium esculentum*, which although not an indicator of silvicultural regrowth forests, was more abundant in these forests.

Table 4-4. PERMANOVA results for model with three factors and eight covariates.

Source	df	SS	MS	Pseudo-F	Estimate of Components of Variation (sq root)
sN20	1	16674	16674	11.89 ***	13.5
sPHW	1	12060	12060	6.87 ***	11.5
cPPD	1	9632	9632	6.87 ***	10.0
CTMX	1	7658	7658	5.46 ***	9.9
sCAL	1	4228	4228	2.01 **	7.6
sPOT	1	3715	3715	2.65 **	5.4
sNWS	1	3216	3216	2.29 *	4.9
sTIN	1	2965	2965	2.11 *	4.5
dAG3) (fixed factor)	2	11198	5599	3.99 ***	13.5
dFF2 (fixed factor)	1	7753	7753	5.53 ***	13.1
mPM2 (fixed factor)	1	1708	1708	1.22 ns	3.1
mPM2 *dFF2	1	3301	3301	2.35 *	10.5
dAG3 * dFF2	2	4536	2268	1.62 *	9.0
mPM2*dAG3	2	1803	901	0.64 ns	-6.8
mPM2*dFF2* dAG3	2	2813	1407	1.00 ns	0.9
Residuals	64	89773	1406.6		37.5
Total	83	183030			

P-values, based on permutations (all ≥ 9898): *** $P \leq 0.0001$, ** $0.001 < P < 0.01$ * $0.01 < P < 0.05$, n.s. $P > 0.1$

Pairwise PERMANOVA test results provided strong evidence that species assemblage varied in response to fire frequency both for near (t = 1.95, DF = 27, P = 0.0004) and far plots (t = 1.76, DF = 29, P = 0.005). Within twice burnt plots there was weak evidence of a difference in assemblage depending on whether the plots were near or further from the boundary (t = 1.56, DF = 24, P = 0.016) but for plots burnt only once the differences in species assemblages between plots near and those far from the mature forest edge could not be distinguished from chance variation (t = 0.99, DF = 32, P = 0.44). Among plots burnt twice, species associated strongly with sites near the edge of mature forest included seven indicators of old growth forest, four of older regrowth or other mature forest while among the species associated with sites further from the edge there were no older forest indicators (Table 4–3). In the analysis of all four combinations of fire frequency and proximity, seven old growth indicator species were strongly associated with plots burnt only once and located near the mature forest edge, while the silvicultural and older regrowth

indicator species *Pomaderris apetala, Acacia dealbata* and *Tasmannia lanceolata* were associated with plots burnt twice or more and near the mature forest edge. Only two species, *Pteridium esculentum* and *Leptospermum scoparium,* were strongly associated with plots burnt twice or more and in situations far from the mature forest edge (Table 4–3). Although neither of these were indicators of a particular forest age class both were more common in silvicultural regrowth.

The interactive effect between age and fire frequency classes was weak ($P = 0.05$, Table 4–4). Species composition for the youngest group of plots (< 40 years) burnt only once differed from plots burnt twice or more ($t = 1.51$, $DF = 12$, $P = 0.01$). There was no evidence that among silvicultural forests, 40 to 50 years of age, that assemblages differed in response to different fire frequencies ($t = 1.34$, $DF = 14$, $P = 0.48$). Among older regrowth forests assemblage differences in response to burning frequency approached the 0.05 level of significance ($t = 1.33$, $DF = 22$, $P = 0.07$). In plots that had only been burnt once, all three age classes had assemblages that were significantly different from each other ($1.48 > t < 1.87$, DF 10 to 24, $0.008 \geq P \leq 0.034$). But among plots burnt twice or more, no age related assemblage differences could be found between the two older plots groups (t= 1.06, df = 14, $P = 0.33$), but the assemblages differed more substantially between the youngest compared to both older forest plots (t = 1.45, df = 16, $P = 0.04$; t = 1.57, df = 10, $P = 0.02$ respectively).

Random forest meta-analysis results

Random forest models developed with inputs of both LC metrics and site variables had higher estimated median p-R^2 than models developed only from LC metrics ($P < 0.01$). The estimated median p-R^2 were also higher for models developed with inputs from both LC metrics and site variables compared with models developed from site variables alone for all plot sets. Most of these differences were distinguishable from chance variation for at least one of the landscape year metric groups (Table 4–5). The only plot set for which there was no significant improvement in results with the addition of LC metrics from either of the landscape years tested was the set including all plots and all species (Table 4–5).

Table 4-5. Association between five different variable sets and species abundance for forest age classes and species groups.

	# of plots	# of species	Variable set: Site	Current Year LC	Following Fire LC	Site & CY LC	Site & FF LC	Grand median
Plot set			Friedman's estimated median pseudo R-squared (sum of ranks). Shared letters denote $P > 0.05$ level (not significantly different)					
Regrowth <110 yrs old	84	59 all	0.21 (189) b	0.12 (137) a	0.10 (125) a	0.22 (219) bc	0.23 (217) c	0.18
YSR & OSR 4-49 yrs old	50	61 all	0.20 (151) b	0.14 (123) ab	0.12 (114) a	0.24 (205) c	0.24 (203) c	0.19
OSR 22-49 yrs old	43	50 all	0.24 (154) b	0.16 (116) a	0.15 (105) a	0.28 (196) c	0.26 (180) bc	0.22
MR 70-110 yrs old	34	54 all	0.22 (154) b	0.13 (117) a	0.14 (128) ab	0.26 (210) c	0.24 (202) c	0.20
Mature >70 yrs old	57	50 all	0.25 (167) b	0.13 (95) a	0.12 (107) a	0.26 (183) c	0.27 (199) c	0.21
Old growth >110 yrs old	23	39 all	0.33 (110) ba	0.32 (105) a	0.24 (82) a	0.39 (148) c	0.35 (127) bc	0.33
All	107	53 all	0.25 (186) b	0.12 (105) a	0.12 (104) a	0.26 (202) b	0.25 (200) b	0.20
Regrowth	84	16 OGI	0.25 (47) ab	0.08 (33) a	0.06 (35) a	0.27 (61) b	0.24 (50) ab	0.18
OSR	43	16 OGI	0.20 (44) a	0.18 (38) a	0.15 (37) a	0.25 (63) b	0.24 (59) b	0.20
Regrowth	84	20 MI	0.25 (66) bc	0.12 (47) ba	0.09 (43) a	0.26 (79) bc	0.23 (66) bc	0.19
OSR	43	17 MI	0.18 (47) ab	0.17 (41) a	0.17 (42) a	0.23 (62) b	0.23 (64) b	0.20
Regrowth	84	14 SI	0.22 (44) ab	0.19 (42) a	0.13 (28) a	0.26 (57) b	0.27 (56) b	0.21
OSR	43	13 SI	0.35 (47) b	0.14 (26) a	0.19 (24) a	0.32 (50) b	0.34 (48) b	0.27

* Association was measured using Friedman's estimated median for pseudo-R squared (p-R2) of all successful Random forest species models (see methods).

Models developed from site variables alone had higher estimated median pseudo-R squared (p-R^2) than models developed from LC variables alone for all plot sets. In

most instances these differences were greater than would be expected by chance variation ($P < 0.05$). However, for models of mature forest and old growth indicator species the differences were less substantial and could not be distinguished from chance variation either for all regrowth or the older silvicultural regrowth plot sets ($P > 0.05$).

Although estimated median p-R2 for models developed from inputs of only LC following fire variables were lower than for models developed from inputs of only Current Year LC variables for most plot sets, the differences were not great enough to be distinguishable from chance variation. Landscape metrics developed from current year landscapes did not provide significant improvement in model performance compared with metrics developed from landscapes following fire when the landscape metrics were combined with the site variables (Table 4–5).

Among the different plot sets, random forest models explained species relative abundance best for old growth plots and most poorly for all silvicultural plots less than 50 years in age. Mann-Whitney test for differences between populations on the basis of results of all successful species within each group provided evidence that old growth plots produced stronger models than any other plot set. Among the other plot sets there was no evidence that model performance differed, although the median result for older silvicultural regrowth plots was higher. There was no significant difference in model performance between any of the plots sets when the same species were compared (Appendix 4.6).

There was almost no difference in the median p-R^2 for models developed from inputs of LC variables of different spatial scales, for any of the regrowth age plot sets (P all > 0.1, df = 3, results not shown). For models developed for the abundance of indicator species of older forest classes within older silvicultural regrowth plots and using site and mature forest LC metrics as candidates, metrics developed from the 500 m scale gave the best results while those generated from the 2000 m scale gave the worst. However, the differences were still not sufficiently different to be distinguished from chance variation.

Random forest models of individual species abundance for older silvicultural regrowth forest

Random Forests successfully produced relative cover models for 40 species (p-R^2>10%) from the older silvicultural plot data when the same reduced set of 47 variables were used as the candidate set (Appendix 4.7). Models for only three of these species did not include any LC metrics among the six most highly ranked variables and only three did not include site variables. LC metrics were also excluded from the best model of all candidate sets for these three species. Other candidate sets without LC metrics produced better models for seven of the species. Fifteen species had either only positive associations with mature forest metrics and/or negative association with other vegetation metrics. Among these species were both species indicators for mature forest (e.g. the dominant rainforest trees *Nothofagus cunninghamii, Eucryphia lucida* and *Atherosperma moschatum*) and silvicultural forest (e.g. *Gahnia grandis*). The nine species that had only a negative association with mature forest metrics or a positive association with other vegetation metrics lacked species indicators of mature forest. Thirteen species had more than one LC metric in the model, including ten ferns (Appendix 4.7).

There were no statistically significant patterns in the selection of mature forest metrics compared with old growth forest metrics although the two most frequently selected metrics were the proportion of old growth forest (16 species) and distance to old growth forest (15 species). Metrics calculated at 500 m and those calculated at 1000 m were similar in their predictive capacity (Appendix 4.8).

Both soil and climate variables were represented among the six highest ranking variables for 19 species models, while disturbance and topographic variables were included among the six highest ranking variables in only eleven and eight species models respectively. Proximity to mature forest metrics (4 metrics) were included in models for 15 species while proportion of area occupied by mature forest classes (16 metrics) were included in models for 27 species. LC metrics representing the proportion of younger forest and non-forests (12 metrics) were included in models for 21 species.

Beta regression and Random forest models of individual species abundance for all regrowth forest

Beta Regression and Random Forests modelling of regrowth plot data was successful for 60 and 41 plant species respectively using available site variables and restricting the LC metrics to proximity to mature forest metrics and mature forest metrics calculated at the 500 m scale. Overall Random Forest modelling provided more successful models for 55 species when candidate sets included additional LC metrics calculated at other scales and for other vegetation classes. Both methods produced successful models for 52 species, eight species were modelled successfully only by Beta Regression and three only by Random Forests. A summary of modelling results is presented for only 40 species, which occurred in 9 or more plots and achieved a pseudo-R^2 of 18% or more for at least one of the modelling methods (Appendix 4.9).

In 73% of all successful Beta Regression species abundance models, mature forest metrics led to model improvement while 63% of species included mature forest metrics in their best Random Forest model. However, there was not always coincidence between the inclusion of these metrics using both methods (Appendix 4.9). Both methods included mature forest metrics in abundance models for only 26 species. Of these, just eleven species were consistently positively associated with mature forest metrics calculated for scales up to 1000 m for regrowth forest plots as well as the older silvicultural plot subset (Table 4-6). Of these eleven species, all but *Eucalyptus delegatensis* and *Hymenophyllum cupressiforme* were indicator species of mature forest. The methods also agreed that, for five species, mature forest metrics did not contribute to model improvement. Among these five were both of the dominant *Eucalyptus* species, *E. regnans* and *E. obliqua*, and the rainforest tree *Eucryphia lucida.* The strength of model improvement due to the inclusion of LC metrics compared with the performance of models without mature forest metrics was correlated between the two methods of analysis ($P = 0.02$, $R^2 = 15.64\%$).

Table 4-6. Summary of model results for species with consistently positively association between abundance within regrowth forest and mature forest metrics.

Method :	Beta Regression (LC metrics)								Best Random Forest results								
	Full model		LCI	Variable groups					Cand	Best	Best	S	LCI	Variable groups					
Species name	AIC	p-R2	%	Mat LC#	Dist	Clim	Soil	Oth	Set^	p-R^2	p-R^2		%	Mat LC	Yng LC	Dist	Clim	Soil	Top
Polystichum proliferum	**-994**	11	**74**	M*			(+)Ca		SLa	25	06		76	17					21 C
Tmesipteris obliqua	-1326	31	26	M*		(+)R*	(+)N*	T*	SMn	30	25		17	14			(+)14 R	+22 N	
Anodopetalum biglandulosum	-1157	19	59	M*		(+)P*	(-)K*		SLf	43	0		100	38			(+)31 P		
Phyllocladus aspleniifolius	-948	43	77	M*		(+)T*	(-)Al		FF	36	0		100	19	(+)18				
Anopterus glandulosus	-1036	16	58	M*		(+)T	(-)N*		CY	42	0		100	34					
Eucalyptus delegatensis	-1352	18	36	M*		(+)T*		N*	SLr	36	16		56	14	(-)11	(-)7 A	(+)14 T		
Nothofagus cunninghamii	-736	59	05	M	(+)F	(+)T	(-)Al	N,D	FFS	40	40		0	16		(+)14 A	(+)15 R	(-)21 Al	
Dicksonia antarctica	-540	33	14	M*	(+)A	(-)P*	(+)N ρ		SMn	31	28		10	15		(+)02 A		(+)31 N	
Hymenophyllum flabellatum	-1171	33	50	M*	(+)A*	(-)P*	(+)ρ		FFS	46	33		28	23	(-)18	(+)29 A			
Hymenophyllum cupressiforme	-1310	10	21	M*	(+)A*	(-)T*	(+)ρ *		FFS	23	12		48	22	(+)22	(+)25 A			
Blechnum wattsii	-805	21	07	M*	(+)F		(+)ρ		CY	12	0		100	23					

Beta regression modelling only attempted to fit 500 m scale mature forest metrics and distance to mature forest metrics

See next page for additional notes relating to Table 4–6

Notes for Table 4–6 continued

^ Candidate sets from which best model was located included Site only (S), reduced site only set (SR) Current year LC metrics (CY) LC metrics following fire (FF) current year LC metrics, Current year LC metrics and site variables (CYS), LC metrics following fire and site variables (FFS), 250 m scale LC metrics and site variables (SLa), 500 m scale LC metrics and site variables (SLn), 1000 m scale LC metrics and site variables (SLf), 2000 m scale LC metrics and site variables (SLr) and mature forest metrics and site variables (SMn).

Relationship to variable groups:
Relationship to topographic & other variables not shown (T: topographic index, N=northness/northwestness, C=curvature variables, D=dominant eucalypt class)
+ve disturbance: abundance increases with forest age (A) and decreases with fire frequency (F)
+ve climate: abundance increases in association with rainfall (P)and declines with temperature (T) and radiation (R)
+ve soil: abundance increases in association with nitrogen (N), conductivity (ρ), calcium (Ca) and declines with increased amounts of Aluminium (Al) and potassium (K).

Random forest models of individual species abundance in mature forests

Of the fifty three plant species with abundance models had a p-R^2 greater than 15% for at least one of the mature forest age classes, only five species, *Cenarrhenes nitida*, *Leptospermum lanigerum*, *Eucalyptus obliqua*, *Monotoca glauca* and *Pteridium esculentum* did not include any LC metrics among the top six ranking variables (Appendix 4.10). However abundance of *Cenarrhenes nitida* in old growth forests and all mature forests was found to be associated with the proportion of old growth forest in the one kilometre radius for both plot groups (Importance Value 21 for old growth and IV 16 for all mature forest) when modelled from 2009 LC metrics and site variables, but this model explained less of the variance in the data (p-R^2 = 0.46 for old growth, and 0.39 for all mature forest plots).

The separation of plots into old growth and younger mature forest classes resulted in a reduction in the number of species models that were successful due to the reduced power of the analysis. Within these two age classes there was no difference in the frequency of plant species for which current year metrics were successful compared with metrics derived from historical landscapes. When the plots were pooled and

analysed together two-thirds of species models were developed from historical LC metrics. There were no patterns discernible in the groups of species for which current year metrics were selected compared with historical metrics.

Fifteen species were either associated with the abundance or close proximity with mature forest in their landscape or associated negatively with the presence of younger forest or non-forest vegetation (Appendix 4.10). All were rainforest species, most of which were indicators of mature forest. They included poorly dispersed species such as *Nothofagus cunninghamii, Eucryphia lucida*, bird dispersed tree species such as *Phyllocladus aspleniifolius*, species with winged seeds such as *Anopterus glandulosus*, and several epiphytic ferns.

Seven species showed the opposite trend, being either associated negatively with the amount of mature eucalypt forest or rainforest in the surrounding area or associated positively with younger forest or other vegetation metrics (Appendix 4.10). These included important silvicultural indicator species *Pomaderris apetala* with a soil stored seed bank and the bird dispersed silvicultural indicator shrub, *Pimelea drupacea* which is known to occur commonly in rainforest). Also included within this group were other rainforest species that were bird dispersed such as *Aristotelia peduncularis* and *Pittosporum bicolor*, which had been identified as indicators of mature forest.

The rest of the 26 species a less clear pattern of association with mature forest metrics and other vegetation metrics, if not in the best model than when the results of the best model were compared with the results from the other candidate set (Appendix 4.10). Many of these were well dispersed species including epiphytic ferns.

4.4.3 Can species traits be used to predict species abundance response to landscape context?

Older silvicultural regrowth forest

Supplementary discussion of the best models produced for species abundance within older silvicultural regrowth forest is provided as part of Appendix 4.7.

The average increase in p-R^2 score for the best models which included LC metrics compared with the best model from among candidate sets without LC metrics was 0.12, but ranged from a reduction of 0.12 to an improvement of 0.42. There was evidence that the model improvement was greater in absolute terms for shade-tolerant species (median improvement = 0.12) than for non shade-tolerant plants (median improvement = 0.03; *Kruskal Wallis H* = 5.51, df = 1, *P* = 0.019, adjusted for ties). Likewise, indicator species for the older forest classes had a higher median improvement compared with those species which were not indicators of these forests (*Kruskal Wallis H* = 4.52, df = 1, *P* = 0.033, adjusted for ties). Resprouters had a higher median improvement in model score compared with non-resprouting species (*Kruskal Wallis H* = 7.4, df = 1, *P* = 0.007, adjusted for ties). However, other plant traits such as dispersal mode, distance of dispersal or the presence of a soil or aerial stored seed bank did not appear to be associated with change in model strength when LC metrics were included. The adjusted LCrI index was found only to be distinguishable from chance variation for resprouting groups and soil-stored seed bank groups but no significant associations were otherwise observed between the plant trait and dispersal mode groups and the LCrI index. In this case non-resprouting plants and plants with soil-stored seed both had a greater negative contribution from LC metrics compared with other plants (*Kruskal Wallis H* = 4.42 df = 1 *P* = 0.036 and *H* = 4.90 df = 1 *P* = 0.027 respectively, adjusted for ties). The IVMA score was also associated positively with older forest indicators and with resprouters (*Kruskal Wallis H* = 6.43 df = 1 *P* = 0.011; and *H* = 4.44, df = 1, *P* = 0.035 respectively, both adjusted for ties). Again there was no discernible relationship between the IVMA score and dispersal mode among the results of Random Forest species models.

The maximum importance value for the mature forest metrics was most associated positively with indicators of older forest classes, shade tolerant species, epiphytic ferns and species without soil-seed banks (*Kruskal Wallis H* = 15.51 df = 4 *P* = 0.004; *H* = 15.67, df = 1 *P* = 0.000; *H* = 15.98 df = 1 *P* = 0.000; *H* = 6.55 df = 1 *P* = 0.010 respectively (all adjusted for ties). Angiosperms associated with older forest classes and which had short dispersal ranges were the species group most associated positively with mature forest metrics (*Kruskal Wallis H* = 23.34 df = 5 *P* = 0.000 adjusted for ties). Short distance and long distance dispersed angiosperms not

associated with older forest classes were the two most negatively associated species groups with mature forest metric importance scores. Ferns had the highest median importance scores among species not associated with older forest classes. Among the older forest indicator species the angiosperms with long distance dispersal mechanisms had the lower median importance scores for mature forest metrics than ferns but the differences in medians among these groups with intermediate importance scores were not distinguishable at an alpha level of 0.05 (Table 4–7).

Regrowth forest

There was no evidence from the Random Forest modelling of individual species abundance in regrowth forest that improvement in model strength due to the inclusion of mature forest metrics was associated with any plant traits such as indicator age-class group, life-form, resprout capacity, regeneration mode, seed persistence mode, or dispersal range (Appendix 4.11). Among the results of the beta regression modelling there was only weak evidence that resprout species were more likely to be positively associated with mature forest metrics (Kruskal-Wallis Test: $H = 3.89$ df = 1 $P = 0.049$, adjusted for ties). Among the subset of species for which modelling was more robust, there was also weak evidence that the LC improvement score (modified by the direction of association) was more strongly positive for indicator species of mature forest and shade tolerant species ($P < 0.05$) but there was no evidence of any association with dispersal range (data not shown).

Table 4-7. Importance of mature forest metrics by plant groups from species abundance models using older silvicultural regrowth forest plots.

		MFI species			Other species				Two group comparison	
		Ferns	**Long range dispersal**	**Short range dispersal**	**Ferns**	**Long range dispersal**	**Medium range dispersal (bradyspory)**	**Short range dispersal (soil seed bank)**	**All Silvicultural regrowth indicators**	**All Fire-sensitive Old growth indicators**
IVMA (same set model)	N=30	8	0	**3**	1	9	3	6	10	3
	Mean	5.6 ± 11.8		**23.0 ± 8.9**	7.0 ± *	-1.0 ± 16.5	23.0 ± 24.2	-7.7 ± 10.4	1.8± 13.6	23.0 ± 8.9
	Median	6		**18.0**	7.0	0	-10	-8.0	1.0	18.0
***H* = 8.64, df = 5 *P* = 0.12**		**a**		**c**	*	ab	abc	**b**	**H = 4.13, DF = 1 P = 0.04**	
IVMA (best model)	N=39	10	3	**4**	1	10	5	6	11	4
	Mean	16.5 ± 8.6	22.0 ± 9.0	**22.5 ± 8.2**	7.0 ± *	3.5 ± 14.1	4.6 ± 11.6	-2.2 ± 5.3	3.7 ± 19.5	22.5 ± 8.2
	Median	16	22	**24**	-17	0	0	0	0.0	24.0
***H* = 3.36 Df = 6 *P* = 0.002**		**a**	**a**	**a**	*	**b**	**b**	**b**	**H = 6.84, DF = 1 P = 0.009**	
LCrI (best model)	**N=39**	10	3	**4**	1	10	5	6	11	4
	Mean	31.1 ± 29.4	65.0 ± 17.8	**19.5 ± 13.2**	10 **± ***	7.9 **±** 27.4	27.2 **± 44.6**	0.7 **± 10.1**	1.5± 49	19.5 ± 13.2
	Median	15.0	71.0	**14.5**	10	0.0	1.0	-2.5	-1.0	14.5
***H* = 15.38, df =6 *P* = 0.02**		AC	AC	**C**	*	B	AB	B	**H = 3.36, DF = 1 P = 0.07**	

4.5 Discussion

4.5.1 Do assemblages vary with age and proximity to mature forest?

Metapopulation theory suggests that the nature of the connections between individual species populations within and between regions is important for their persistence (Levins 1969; Hanski 1998). Natural and anthropogenic fragmentation of landscapes impacts on connectivity between populations, which may result in local and regional population change including species extinctions (Hess 1996). For such processes to apply to vascular plant species within intact forest landscapes this study assumed that it was necessary that the region comprised a spatial or temporal mosaic of vegetation communities in which islands or gradients in population age occur. Age-related spatial variation in forest communities is common within intact forest landscapes around the world (e.g. Franklin et al. 2002; Amici et al. 2013; Grau 2004).

It was demonstrated in chapter 2 that a mosaic of forests of different ages occur within the study area as a result of past patterns of wildfire and logging, and also that there has been a change in the spatial arrangement and sizes of disturbance patches through time. The present chapter tested and confirmed the assumption that forest age in the secondary forests in this study area is associated with floristic compositional differences, a pattern consistent with findings for other *Eucalyptus regnans* and *E. obliqua* forests (Serong and Lill 2008; Ashton 1976; Hickey 1994), wet eucalypt forest more generally (Brown and Podger 1982a; Noble and Slatyer 1980) and other secondary forest ecosystems around the world (for example the oak forests of the Meditteranean, Amici et al. 2013). The age-related differences observed were consistent with increasing abundance of rainforest species capable of regeneration within shaded understoreys. The importance of stand-age has also been reported for the abundance of *Nothofagus cunninghamii* in Victoria *E. regnans* forests, where modelling has also shown its strong association with gullies and locations with the high rainfall in the warmest quarter (Busby 1986; Lindenmayer et al. 2000b). Sclerophyllous and other pioneer species within the forest understorey show the opposite trend with forest age, most becoming less frequent and abundant. However, while the frequency and cover of dominant eucalypts declines with time they continue

to account for the largest portion of the forest biomass for their life-span of up to about 500 years (Wood et al. 2010; Jackson 1968; Turner et al. 2009). After the eucalypts senesce, the forest becomes climax rainforest comprising species capable of regeneration in the absence of catastrophic landscape-scale disturbance. Some studies have observed that the common broad-leaved pioneer tree, *Pomaderris apetala,* is capable of continuous regeneration in fire-protected dry gullies and scree slopes of eastern Tasmania (Pollard 2006). It is therefore possible, that, even within high rainfall regions, that on skeletal, carbonate-rich soils the rainforest trees *Nothofagus cunninghamii*, *Atherosperma moschatum* or *Eucryphia lucida* may be physically excluded where *P. apetala* can dominate.

In interpreting floristic differences associated with age and some other LC metric related in this study it is important to acknowledge that the forests regenerated since 1960 were mostly subject to clear-fell burn and sow, a treatment not used prior to this. However, among the older silvicultural forests, those last disturbed in 1967 or 1968 were all subject to wildfire with most either logged in the previous few years or just after as part of salvage logging operations. The older regrowth forests were all subject to wildfire with only some having been selectively harvested. This was justified on the grounds that, while the oldest and youngest forests in the study were substantially different, there was little difference between the older silvicultural forests and older regrowth, despite them having been subject to different disturbance types. The same justification was used by Serong and Lill (2008) for their work. Hickey (1994) also observed that mixed forests disturbed by logging retain similar frequencies and abundance of common woody plant species as comparable sites disturbed by wildfire, although he did report that the frequencies and species richness of epiphytic ferns was lower and the richness of ground ferns and abundance of the pioneer sedge *Gahnia grandis* was greater in harvested regrowth forest compared with forests burnt by wildfire (Hickey 1994). Another substantial difference occurring in response to disturbance type differences is that the survival of mature, hollow bearing eucalypts is substantially lower for most clear-felled areas, although in some operations old growth trees unsuited to paper production processes or sawlog were retained. The loss of old growth trees has significant conservation implications for a wide diversity of

fauna, and potentially more subtle environmental and competition differences for vascular understorey plants (Turner et al. 2009; Lindenmayer et al. 1991).

Given that there is a gradient in species abundance with age and the fact that the study region comprises a mosaic of different secondary forest ages, it is assumed that rainforest and old growth forest patches represent islands with the largest source populations for rainforest plant species (*sensu* Jarman and Brown 1983). The extent to which these mature forest habitat islands influence the successional trajectory of disturbed patches is the principle concern of this chapter.

4.5.2 What variables are the best predictors of floristic response – landscape context metrics or site variables?

To date the landscape ecology literature has been strongly focused on the impacts on biodiversity and population dynamics within the remnant stands caused from natural and anthropogenic fragmentation. This study substantially differs from this literature by focusing on the importance of the function that retained mature forest has in the recovery of populations within disturbed native forest patches. The probable mechanisms of mature forest influence have been described in detail by Baker et al. (2013b).

A constraint in the present study is the lack of accuracy inherent in the data collection due to multiple observers and the difficulties in estimating plant cover accurately. Although the issues of observer bias and lack of accuracy were addressed by converting the data to relative cover, there remains a large uncertainty in the accuracy of the relative cover estimates, which inevitably undermine the confidence with which the models can be relied upon. Despite these constraints the inclusion of LC metrics improved model strength for about two-thirds of common plant species over and above models with site variables alone within regrowth forest communities. This was evidence that species abundance dynamics in wet eucalypt forests is being influenced by the extent and proximity of mature forest in the landscape. Among the species showing a response in abundance to the LC metrics it was found that, on average, these metrics accounted for as much as a third of explained variance in species abundance. However, a portion of the explained variance is likely to be shared effects

derived from either correlations with, or interactions between, LC metrics and site variables, which will have caused an over-estimate of the real importance of LC (Borcard et al. 1992; Cushman and McGarigal 2004a; Dormann et al. 2013).

Cushman and McGarigal (2004b) have observed that the coding of response variables will impact on the strength of association measured with LC metrics. This issue was explored using Random Forests Modelling and while the importance of LC metrics was greater and the overall models stronger, there was no evidence that the ratio of LC metrics importance to site variable importance changed. However, by choosing to present results for cover abundance, it should be remembered that the results presented are therefore conservative estimates of the strength of association between species and LC.

McGarigal and McComb (1995), in a study similar to this one, investigated the effect of varying the proportion of late-seral forest in the landscape on the abundance of 15 late-seral forest birds within the Oregon Coast Range in landscapes comprising a mosaic of native forest patches of different ages due timber harvesting. They found, as in this study, that species showed a wide range of response to LC. Among the two-thirds of birds which showed a significant response to LC, on average LC accounted for only a little over a third of their variance. The similarity of their results with those in this study further strengthens the likely veracity of both.

It is apparent from the results here that, on their own, LC metrics were generally poorer predictors of plant abundance than site variables. This would not have been the case on a featureless and uniform plain, so that the proportionate contribution of landscape effects is dependent on the degree of environmental heterogeneity and the degree of response of the vegetation to this environmental heterogeneity. Cushman and McGarigal (2004a) also reported that plot level differences (especially vegetation differences) explained a far greater portion of the variance in bird assemblage in the Oregon Coast Range than LC. This result is no surprise since the environment at the site and the adaptive traits and competitive strengths of each species will substantially determine which species will be able to establish and survive competition from others at the site (Austin 1985; Austin et al. 1997). However, this study very clearly shows

that where the local site factors are sufficient to support species establishment, LC is able to influence abundance of numerous species both positively and negatively.

Among the model results for individual species common in forest over 70 years old there was a tendency for species more common in silvicultural forests (e.g. *Pomaderris apetala*) to be negatively associated with increased abundance of mature forest in surrounding landscapes. One interpretation of this result is that mature forest in areas more frequently disturbed have a themselves a history of higher fire frequency and therefore tree falls result in the germination of seed of pioneer species from the soil seed bank. In such forest landscapes the sources of pioneer species with good dispersal capacity is likely to enable these species to establish more readily in any disturbance gaps. In contrast, the richness and diversity (data not shown) of communities and the abundance of many hygrophilous rainforest species (e.g. *Eucryphia lucida*) were positively associated with abundance of mature forest in the surrounding landscape. *Nothofagus cunninghamii* was most strongly associated with the abundance of rainforest vegetation in historical landscapes. Within mature forest, the large number of species (nearly half) that had contradictory associations with different LC metrics or were not associated included long-lived species, species with good persistence or dispersal capacity or species and those well adapted to growth in both mature forest and early successional forest communities (Appendix 4.10). These results suggest both that composition of mature forests is in part a legacy determined by the LC of the patch when it was last burnt and that there may also be an ongoing influence from LC on the persistence and abundance of some species in later stages of forest development.

4.5.3 What is driving the observed response to landscape context in these forests?

LC has been shown to influence species abundance and diversity patterns in many and complex ways (Saunders et al. 1991; Lindenmayer and Fischer 2006). In theory distance to propagule source and patch size both have the capacity to regulate species colonization success directly and indirectly (Amarasekare and Possingham 2001; MacArthur and Wilson 1967). These effects have been demonstrated in experimental

old-field situations and indicated through theoretical simulation modelling (Liu and Ashton 1999; Yao et al. 1999; Hokit and Branch 2003; Cook et al. 2005).

The arrival at the site by all colonists, whether early or late succession plant species, is regulated by dispersal capacity and distance to the nearest propagule sources (Yao et al. 1999; Cook et al. 2005). After establishment, abundance is only likely to be regulated by these mechanisms if the ongoing arrival and establishment improves the competitiveness of the species along the gradient of colonist-competition continuum (Tilman 1993; Cook et al. 2005). Among empirical studies for tropical forests Grau (2004) showed that distance to other disturbance patches was a significant predictor of differences in pioneer communities within secondary forests in the topics, and Laurance et al. (1998b) found distance to the patch edge and forest age also influenced tree recruitment rates. In dry forest grasslands Löbel et al. (2006) found that distance was able to explain some of the variation in bryophyte and lichen communities, but not vascular plants.

Many plant species colonization of a site is dependent on dispersal by birds or other vertebrates (Neilan et al. 2006; Cacallero et al. 2013), making them dependent on visitation rates by vector species. Factors that have been identified as facilitating the recovery of bird assemblages following disturbance include the presence of biological legacies such as live and dead trees, logs and other perching or roosting places (Taylor and Haseler 1995; Toh et al. 1999; Franklin et al. 2002; Elgar et al. 2014). The rate of recovery of fleshy-fruit bearing plants at the site may also feedback to the rate of recovery of frugivores to the site (Neilan et al. 2006), which in turn may influence the arrival of other fauna. Various studies of birds within Australian eucalypt forest and woodlands have also demonstrated that birds are sensitive to the landscape context: with greater richness of birds occurring in sites with landscapes that have a greater proportion of native vegetation within their landscape, a lower proportion disturbed by fire, and which is closer to areas of core habitat vegetation (Tubelis et al. 2007; Lindenmayer et al. 2009; Lindenmayer et al. 2014b; Cunningham et al. 2014). Nevertheless, within the present wet forest region, studies have demonstrated that some mature forest bird species rarely utilise young regrowth forests (<7 years old) despite the proximity within the site of retained mature forest elements or landscapes with an abundance of mature forest (Lefort and Grove 2009;

Hingston et al. 2014). Habitat quality at the site may well be an essential pre-requisite for a response to landscape context to become evident. Within a study of birds undertaken concurrently with the vegetation surveys for the present study, there was evidence that bird numbers, species richness and numbers of several individual mature forest bird species were positively associated with the level of forest maturity in the surrounding landscape at older silvicultural regrowth sites (Wardlaw et al. 2012). Given an association between bird visitation and colonization rates of some plant species, the association with mature forest metrics observed for some plant species may be an indirect effect of the response of their fauna vectors to landscape context.

Although there was an expectation that the longer dispersal range of bird-dispersed species may result in their being less sensitive to landscape context, the results found in this study were that many of the common bird dispersed species (e.g. *Tasmannia lanceolata*, *Pittosporum bicolor* and *Phyllocladus aspleniifolius*) had a similar positive association with mature forest metrics as mature forest plant species with more limited dispersal capacity. Evidence for an association between these species and LC metrics was often restricted to data including older silvicultural regrowth and or older regrowth but was not evident within the small group of younger aged silvicultural regrowth forests. More work is needed to determine to what extent the sensitivity of fauna to habitat quality and landscape context is driving the response of these plant species.

Species with a seed supply regulated not by the presence of surrounding forest but by the historical establishment of a soil or aerial seed store are able to germinate directly after disturbance. It was initially thought that these species might be independent of LC influence. However, the results suggest that even these species are affected by LC since many were less abundant in areas close to mature forest, presumably in response to the increasing success of rainforest species at the edge, where rainforest species have an abundant seed supply.

Among the species occurring in greater abundance in forest close to mature forest boundaries were the four rainforest trees *Nothofagus cunninghamii, Atherosperma moschatum, Phyllocladus aspleniifolius* and *Eucryphia lucida*. This agrees with the

findings of Tabor et al. (2007) for seedling numbers for these same four rainforest tree species. In addition the results here show at least four other rainforest species have a similar response to LC. Tabor et al. (2007) suggested that gradients in microclimates, soil nutrients, and competition are all likely to have contributed to the observed response to LC. This seems likely, as does their suggestion that the cause in decline with distance of species abundance is most strongly driven by the reverse exponential decline in seed numbers with distance from source trees. They noted that declines in seedling numbers over the distances they measured were consistent with results of Hickey (1982) showing declines in seed capture rate with distance from parent trees for two of these species (*E. lucida* and *N. cunninghamii*). Tabor et al. (2007) also observed that the differences between species in both the rates of decline with distance and differences in seedling densities associated with the different directions from the boundary, were consistent with the seed dispersal mechanisms of each species.

The results for *Atherosperma moschatum*, although in keeping with that of Tabor et al. (2007), are contrary to the usual expectation of a wind dispersed species. *A. moschatum* most typically reproduces by resprouting (Read and Brown 1996), and although the seed is wind dispersed and capable of dispersing over great distances, the majority falls beneath the parent tree (Hickey et al. 1983). The rarity of seedling establishment has also been attributed to browsing pressure due to its high palatability (Neyland 1991). Therefore, although this species may have the opportunity to establish further from the boundary from mature forests than poorly dispersed *Nothofagus cunninghamii*, the low arrival rates of seeds beyond 50 m from mature trees, and the high chance of being browsed would make such establishment events relatively rare over time periods measured in years and decades.

4.5.4 Did landscape context influence the dominant canopy species?

Eucalypt species are known to be strongly competitive across the environmental gradient and understorey assemblage variation is commonly associated with differences in the dominant eucalypt due to a number of interactions between the synusiae and environment (Kirkpatrick et al. 1988; Austin et al. 1997; Kirkpatrick

1997). In Victoria and Tasmania *Eucalyptus regnans* occupies a relative narrow environmental niche in which soils are at least moderately fertile and climates are relatively cool and wet (Williams and Potts 1996; Ashton 1981a). In contrast *E. obliqua* has a greater tolerance for poorer rocky soils and a warmer- drier climate (Ashton 1981a). The results of this study demonstrated that for this area of the southern forests in Tasmania, *E. obliqua* is also more abundant than *E. regnans* in the highest rainfall sites, a trend which is evident across Tasmania, with *E. obliqua* replacing *E. regnans* in importance in the far west and northwest of Tasmania. Both species are largely absent from the far southwest of the state (Williams and Potts 1996). The bimodal distribution of *E. obliqua* with respect to climate suggests that it is excluded from sites where *E. regnans* has its greatest productivity. The factors apparently excluding *E. regnans* from some high rainfall sites requires further examination. The distribution of soil types, and fire histories associated with high rainfall areas occupied by *E. obliqua* compared with *E. regnans* require further investigation. Preliminary results of climatic modelling for these species (data not shown) suggests that the ratio of radiation to moisture availability may be important in determining which of these species dominates at a site. *E. regnans* had a higher probability of occurring at sites with a higher ratio of radiation to rainfall compared with *E. obliqua*, at least within high rainfall areas.

The dominant eucalypts, *Eucalyptus regnans* and *E. obliqua*, were among the few species in regrowth forests that showed no association with mature forest metrics using either modelling methods. This result was expected given that these trees generally survive wildfire and their seed is artificially sown following timber harvest operations. However, the results from Random Forest modelling with older silvicultural forest plots showed there was a negative association between *E. regnans* and non-forest metrics and *E. obliqua* and mature forest metrics. The negative association of *E. regnans* with metrics describing the abundance of agricultural land, plantations and other non-forest vegetation may be an artefact of the targeting of *E. regnans* forest sites for clearance for plantations and agricultural land. *E. regnans* forests are also likely to be less common in landscapes with larger amounts of native non-forest due to the higher fire frequencies and lower soil fertilities associated with these vegetation types within the study area (Corbett and Balmer 2001). The negative

association between *E. obliqua* and mature forests within older silvicultural plots is more perplexing, although it does suggest that there may be reduced canopy importance relative to the understorey in response to root competition, shading or increased herbivory pressure associated with the mature forest edge. While it is possible that there is a real negative effect from the proximity and abundance of mature forest on the abundance of *E. obliqua,* I would have expected that the depth of this influence would be too small to detect at the scale sampled, since the majority of plots were located at distances greater than 50 m from the boundaries of mature forest patches, a distance at which root and canopy competition is likely to have substantially reduced. Differences in the rates of herbivory (above and below ground) may well extend beyond 50 m and the effects of this pressure on the success of *E. obliqua* are deserving of further investigation. Differences in species distributions elsewhere have been reported to be associated with patterns of herbivore activity and preferential species selection for browsing (e.g. Cremer 1969; Neilson and Pataczeck 1991; Saunders et al. 1991; Wahungu et al. 1999; Bulinski and McArthur 2000; Cadenasso and Pickett 2000).

4.5.5 Why was patch size unimportant?

For comparative purposes patch metrics were included in the initial analyses. The results demonstrated that size of patches were unimportant in the regulation of species assemblage variation and individual species abundances, although it was associated with some richness and diversity metrics (data not shown). It is probable that the large patch sizes generated by historical clear-fell operations and by wildfire in this region are well over the threshold at which most species might be excluded from colonization (Yao et al. 1999). The result is also in agreement with the observation by Fahrig (2013) that the total available habitat area within an appropriately sized landscape may be a better predictor of species distributions than individual predictors such as patch size and isolation. It is also likely that for this study area, the correlation between patch-size and the mature forest metrics reduced the value of patch size as a predictor for species abundance and assemblage modelling.

4.5.6 At what temporal scale were the strongest associations?

This study was unable to detect a general trend in preference for metrics derived for either current landscape or the landscape following fire for either species in general or within particular groups of plants. However, the high co-linearity between mature forest metrics generated at these two temporal scales, the relatively small data set, and the complexity of processes driving plant abundance would explain the absence of apparent links between temporal scale and plant abundance. These results should not be used as evidence for a lack of species response to temporal variation in landscape.

There are sound hypothetical reasons why temporal scale variation in LC may be important in the regulation of species abundance responses. This is discussed in the next chapter.

4.5.7 At what spatial scale were the strongest associations?

In the Random Forest analyses there was no overall difference in models developed from LC metrics derived from different spatial scales. Other studies have shown that individual species show a wide variety of responses to differences in landscape scale, so this result was not surprising. However, this study also showed no difference in responses to landscape scales among groups of species with particular persistence and/or dispersal traits or habitat preferences. This was contrary to results in chapter 3 and other landscape studies. Limitations of the data are discussed in chapter 7.

4.5.8 Is there evidence to suggest that competitive exclusion prevents landscape context influence from operating?

Each species might be expected to respond to disturbance, competition and stress in individual ways, giving rise to species specific distribution patterns through space and time due to successional processes and LC influence (Pulsford et al. 2016). Nevertheless, there are only two mechanisms by which a plants species may come to occupy a recently disturbed site: either by being a biological legacy of the previous vegetation at the site (Franklin et al. 2000) or by arriving as a colonist from more distant population sources (Egler 1954; Connell and Slatyer 1977). The presence of the first group of species, which include survivors, resprouters and plants with

persistent seed banks at the site, may competitively exclude or inhibiting the establishment of colonists by being able to rapidly occupy and/or alter site conditions (Egler 1954; Connell and Slatyer 1977; Tilman 1993; Cook et al. 2005). Results for modelling of *Pomaderris apetala* suggest that this species may provide an example of the process of competitive exclusion within these forests. At least for the older silvicultural forests in this region, there was evidence that the distribution of *P. apetala* was independent of LC effects.

Pomaderris apetala establishes after disturbance from a prolific and persistent soil seed bank in areas it has previously occupied. This gives it a competitive advantage where environmental conditions are suitable for its growth. High relative covers of *P. apetala* explain the low diversity scores associated with forest understoreys dominated by this species. Ashton (1975b) reported that *Pomaderris aspera*, a closely related species, concentrates calcium in its leaves, which leads to high calcium levels in leaf litter and surface soils. It is likely given the association between *P. apetala* and soil calcium in the results of this study, that *P. apetala* is also able to alter soil conditions and promote conditions in which it is able to out-compete other understorey species.

The success of *Pomaderris apetala* on fertile soils provides a possible explanation for the modelled association between *Nothofagus cunninghamii* and soil aluminium, since soil aluminium and soil calcium were negatively associated. This contrasts with the expectation that *N. cunninghamii* should be more abundant where soils are fertile and propagule sources are available (Read and Brown 1996). In rainforests of lower soil fertility *N. cunninghamii* is less abundant, occurring as it does in such soils in a mixture with *Eucryphia lucida* and *Atherosperma moschatum* (Kirkpatrick 1977; Read and Hill 1985a; Read and Brown 1996).

The model for *Pomaderris apetala* developed from all regrowth aged plots had a positive association with the proportion of older regrowth forests (60 to 110 years old) in the landscape following fire. Such mature-regrowth forests often retain a high proportion of *P. apetala* within their understorey and this may act as a seed source. Given the rarity of regeneration by *P. apetala* observed within closed forest understoreys, the capacity to colonize new sites would only exist in the immediate

decade following disturbance, or more rarely, after localised tree fall or canopy senescence. This species has no long distance dispersal mechanism and so must rely on incremental boundary expansion into adjacent disturbed sites. The association of *P. apetala* with this particular metric is likely to be at least partly derived from the shared effects, or auto-correlations of this metric with patch size of the last disturbance (wildfire area), fire frequency and negatively with forest age. All these variables were individually correlated with both *P. apetala* abundance and the LC metric 'proportion of older regrowth forest'. The abundance of *P. apetala* is clearly favoured by widespread and frequent disturbance, but it is also dependent on relatively high nutrient status of soils in order to out-compete other understorey species.

4.5.9 Conclusions

These results suggest that landscapes partially logged at the coupe and coupe aggregate scales of 30–300 ha and subject to occasional widespread fire do exhibit landscape effects on the species composition and individual species distributions at a century time scale. The data examined provided evidence that both pioneers and mature forest species are associated with LC, with the former negatively associated with mature forest metrics and the latter positively associated with these metrics, although the response to LC was usually weaker than the responses to the environmental characteristics of the site, including disturbance history. Dispersal characteristics were not strong drivers of the observed responses with the strength of responses varying greatly between species. There are many ways in which LC may be directly and indirectly affecting species distributions in these forests, but the results suggest that LC patterns may provide an indirect means of monitoring the potential variation in abundance of mature forest and pioneer species. The results suggest that maintaining a heterogeneity in LC patterns across the region, but in particularly ensuring the maintenance of mature forest habitats is important for regional biodiversity conservation.

"Human beings, who are almost unique in having the ability to learn from the experience of others, are also remarkable for their apparent disinclination to do so."

Douglas Adams and Carwardine, Mark (1990) *Last chance to see.* Heinemann, London, 208 pp.

Chapter 5 Temporal scale of floristic response to landscape context

5.1 Abstract

This chapter tests the hypothesis that landscape context (LC) will have its greatest influence on the successional trajectory of Australian wet eucalypt forest immediately following disturbance. Disturbance is often associated with a higher than average rate of species mortality and the immediate post-disturbance period is associated with higher rates of colonization than average for a site. The manifestation of landscape influence is therefore likely to peak in response to such perturbation. Landscape Context Index (LCI) metrics were calculated for the landscapes of sampled sites at three time periods: current year, year following fire and the year before the last disturbance. Forest assemblages for three age-classes (<50 years, >70 and <110 years old) were tested using PERMANOVA to determine which of the metrics explained assemblage variation. Mixed effect models were used to test which these metrics explained the greatest variation in the richness of plant species groups and cover of mature forest species within silvicultural regrowth.

The LCI metric calculated for the year following fire provided the best explanation of assemblage variation for all ages of forest tested. But of the various richness and cover responses tested using mixed effect models only the cover of mature forest species was consistently best explained by historical LCI metrics. The high degree of autocorrelation between the temporal scales of the LCI metrics may have contributed to the ambiguity in the results, but the associations observed for some of the richness responses with metrics derived from current year landscape may also provide evidence of an ongoing influence of the landscape following disturbance, particularly on mature forest species colonization. Limitations due to the sampling design made it difficult to distinguish between historical and current year landscape effects in this study. It is recommended that future landscape ecology research consider past and present landscape patterns within their sampling design to better discern the temporal scale of LC influence.

5.2 Introduction

Auffret et al. (2015) noted that the influence of temporal connectivity of landscape on is as important for determining species distributions as spatial aspects of structural (physical landscape units) and functional (e.g dispersal vectors) connectivity of landscapes. Auffret et al. (2015) used the term 'temporal functional connectivity' and defined it as the capacity of species to persist through time in the same place. Examples of this include the ability of some species to persist through disturbance in remnant patches by regenerating vegetatively or from persistent seed banks. Wet eucalypt forests include many pioneer species with persistent seed banks, while the rainforest or mature forest species of these forests often rely on vegetative reproduction. Depending on time periods examined longevity might be another mechanism by which species achieve temporal functional connectivity, and in the wet forests both the dominant canopy and sub-canopy rainforest trees are long-lived (> 300 years).

It may be useful to extend the concept of temporal connectivity (*sensu* Auffret et al. 2015) to spatial aspects of temporal connectivity, by expanding it to include the duration, or temporal scale at which past landscapes continue to influence the biodiversity of the patch. The term 'temporal spatial connectivity' may be appropriate for this concept. However inevitably the structural and functional connectivity within landscapes and their temporal functional connectivity will all strongly influence the temporal spatial connectivity, these four aspects of fragmentation being interactive in their effects on biodiversity.

The lag in response of plants to landscape change has been a focus of several empirical studies that have followed since the development of a mathematical model to predict 'extinction debt' (Tilman et al. 1994). These provide some evidence that the legacies of past landscapes can be as important as patterning in the present landscape in influencing current plant species distribution and abundance. Swift and Hannon (2010) suggest that biodiversity responses are typically likely to be non-linear in their response to LC change. Reasons for this include the interactive effects of habitat loss and fragmentation where habitat loss is extreme and the remaining habitat is subject to both isolation and edge effects (Swift and Hannon 2010). In these situations

competition stress will be greater, especially from invasive species, mortality rates of native species higher, and colonization rates of native species lower. The Allee effect (Allee 1931) may further compound population changes resulting from LC influence. For example, plants occurring in lower population densities may have lower rates of reproductive success (Amarasekare 1998; Chen and Hui 2009; Swift and Hannon 2010). The interaction between all these factors and stochastic disturbance events may lead to sudden change, threshold responses and other non-linear responses to habitat loss (Swift and Hannon 2010). Given the possible importance of threshold effects, in continuous native forest it is probable that historical landscapes may often be more important in explaining current species distributions patterns. Despite this, there has been little attention given in the fragmentation literature to the question of whether the LC at the time of disturbance might be more strongly influential in setting the trajectory of succession in a disturbed patch than later landscape changes that may take place.

Empirical studies of grasslands have demonstrated that lags sometimes occur in the responses of grassland plants to landscape change. For example, Lindborg and Eriksson (2004) reported that the diversity of Swedish grasslands was associated not with current landscape patterns but with landscape patterns from 50 to 100 years ago. Another study found that the lag in grassland plant richness response only persisted until less than ten percent of the landscape. When grasslands habitats were reduced to below this level, species richness patterns in vascular plants reflected current landscape patterns (Cousins 2009). Grassland studies have also demonstrated that the response of species to LC varies, for example species richness of long-lived plants was found to be associated more with past land-use patterns than current landscapes (Krauss et al. 2010). Koyanagi et al. (2012) found that life form, flowering time, and dispersal mechanism may be important determinants of the likely spatial and temporal scale at which plant species respond to the landscape. Richness of both the early-flowering short-forb species and the wind-dispersed late-flowering tall-forb species were associated more strongly with historical landscape patterns (1950s) and to the amount of grassland habitat in landscapes measured at scales of > 1 km^2. Other plant groups (non wind-dispersed late-flowering tall forbs; grasses and sedges; and woody vines and shrubs) showed no particular association to either temporal or spatial scale

and were much more weakly associated with the amount of habitat in the landscape (Koyanagi et al. 2012).

The lag in plant species responses to changing landscapes has also been demonstrated for forest plants. In a study of two fragmented forest regions in Europe,Vellend et al. (2006) report that models of patch occupancy developed for slow species (low rates of colonization and extinction) within a region fragmented for several centuries consistently under-predict occupancies for a more recently fragmented region. In contrast, the models for fast species performed well for both regions. They conclude that slow species are more prone to the accumulation of an extinction debt. Similarly, in a study of lower montane rainforest in southeast Brazil, Metzger et al. (2009) observed that both richness and abundance of shade-intolerant canopy tree species was more strongly associated with historical patch sizes compared with current patch sizes. Hence there is a greater connectedness with historical landscapes where species are long-lived, slow-species, or persistent.

Temporal spatial connectivity may also be a useful concept for explaining the distribution and stability of biomes, including temperate wet eucalypt forests, given the evidence from phylogenetic studies that spatial connectedness provides a strong influence on genetic evolution. Simulations of the impact of landscape barriers on responses in genetic patterns demonstrated that new barriers to gene flow may be detected in some species in a very short time (1-15 generations), and that old barriers may still be detectable in some species more than 100 generations after discontinuities have been removed (Landguth et al. 2010). There is inevitably a feedback between the ongoing evolution of species and the assemblages that develop at the regional scale (biomes) which in turn affects the probability of colonization success of new species arriving from elsewhere (Crisp et al. 2009). Moncrieff et al. (2015) concluded that historical factors (e.g. the geographical connections between regions) are likely to have been at least as important as climate in driving the present distribution of biomes.

The response of each vascular plant species to particular temporal and spatial scales of mature forest influence is likely to vary. In particular, dispersal limits, relative rates of propagule arrival, and tolerance of micro-environmental variation are likely to

affect their competitive capacity, reproductive and colonization success (Baker et al. 2013b). To study the temporal association between LC and the vegetation response in wet eucalypt forest, the Landscape Context Index (LCI) metric is used as a surrogate for LC. This metric weights the surrounding landscape on the basis of forest maturity within a specified radius. The method follows the general approach used to calculate the Landscape Development Intensity index (Brown and Vivas 2005). This metric is described in detail in the second chapter of this thesis, where it was used to describe landscape change since 1947 within the study area. The efficacy of this metric in explaining variation in wet forest floristics is compared with proximity to mature forest (PM), a simpler metric to calculate, but which does not provide an indication of the abundance of mature forest in the surrounding landscape.

This paper tests the hypothesis that landscape context (LC) will have its greatest influence on the successional trajectory of Australian wet eucalypt forest immediately following disturbance. To test this LCI and PM metrics were generated at several temporal and spatial scales. The association of several floristic responses were tested to determine at which scale provided the strongest association. These responses were tested separately for different forest age classes to determine whether the response to LC in wet eucalypt forest was affected by stand demography.

5.3 Methods

5.3.1 Landscape Context Index (LCI) mapping

The study region is described in chapter 2. Vegetation maps comprising 10 vegetation classes (see chapter 2) were prepared for the years 1924, 1950, 1974, 1985, 1996 and 2009 (chapter 2). For each vegetation map an LCI score map was derived for each 50 by 50 m pixel at two spatial scales, 500 m radius (LCI:½k) and 1 km radius (LCI:1k) (chapter 2).

5.3.2 Floristic response variables

The vegetation sampling method for 107 plot sites is described in chapter 4. Of these 107 plots, two were excluded because they were located beyond the region for which LCI maps had been prepared. The final vegetation data set comprised absolute

percentage cover estimates for each plant species observed within each of four or five 10 by 10 subplots sampled within each of the 105 plots (~50 x 50 m in area). The data for all orchid species were excluded from the final data set.

The subplot species presence and cover abundance data were used to derive several floristic response variables for plots grouped according to the forest age (Table 5-1).

Table 5-1: Floristic response variables calculated and tested for each forest age class

	plots grouped into forest age classes:		
Floristic Response	**All silvicultural regrowth** (< 50 years)	All regrowth (< 110 years)	Mature forest (>70 years)
1. Species assemblage	☑	☑	☑
2. Cover of Mature forest indicator species (MFI)*	☑		
3. Total species richness	☑		☑
4. Richness of MFI species	☑		
5. Richness of epiphytic fern species	☑		
6. Richness of woody pioneer species*	☑		

*The method of allocation of species to mature forest indicator species and pioneer classes was described in chapter 4.

5.3.3 Environmental and landscape metric data

A hand held GPS unit was used to record the grid references for one or more of the 50 by 50 m plot corners. The grid coordinates of each subplot centre was derived for each subplot based on the distance and direction measured from a plot corner.

For each subplot, ARC GIS was used to extract the LCI score for each of the six vegetation map years calculated at two spatial scales as well as all other digital environmental data (see chapter 3 for data sources and more detailed methods). The data from these were then used to determine LCI metrics at three temporal scales relevant to the successional development of each plot, i.e. LCI score for the map year prior to disturbance (LCI:BF); the year following disturbance (LCI:FF); and 2009 which was used to represent the current landscape of the plots since it was the year closest to when the plots were surveyed (LCI:CY, Table 5–1). It was not possible to

obtain LCI metrics for all temporal scales for all plots, since vegetation mapping could not be extrapolated further back than 1924. The LCI:BF and LCI:FF for forests burnt prior to 1914, which required vegetation maps for time periods earlier than 1924, were replaced with the LCI scores derived from the 1924 vegetation map instead (Table 5–1).

Table 5-2. Vegetation map year used to calculate temporal scale Landscape Context Index (LCI) metrics for plots grouped according to the year they were last disturbed by fire.

(Years underlined indicate situations where the earliest or latest vegetation map are used as a substitute for a vegetation map year that was not available.)

	Temporal scale of LCI metric:		
Years in which plots were burnt	**Before Fire**	**Following Fire**	**Current Year**
~major fire year	LCI:BF	LCI: FF	LCI:CY
Before 1894	1924	1924	2009
1894–1924 ~ 1898	1924	1924	2009
1925–1947 ~1934	1924	1947	2009
1948–1974 ~1966–68	1947	1974	2009
1975–1985	1974	1985	2009
1986–1996	1985	1996	2009
After 1996	1996	2009	2009

Up to four log transformed proximity to mature forest metrics (PM) were calculated for each plot depending on the plot age class (Table 5–2). Two classes of mature forest were mapped. One named here for convenience as old growth forest (OG), was defined to include forest habitats with a high proportion of rainforest species in the understorey. This class included forest mapped as eucalypt forest that had no history of fire (based on fire history mapping and the absence of eucalypt regrowth). The age of this forest ensures that pioneer species in the understorey would have been replaced by rainforest species. The other forests included in this category were areas mapped as rainforest or as containing myrtle (*Nothofagus cunninghamii*). The other category of

mature forest (MF) included any wet sclerophyll forests burnt in the last century that contained a legacy of mature eucalypt trees with more than 5% cover of eucalypts.

Table 5-3. Four proximity to mature forest metrics (PM) and their definitions (see text for more details).

Code	Metric name: definition
PM	Proximity to mature forest metric: defined as the log transformed distance to nearest mapped patch of mature forest (see MF and OG forest definitions in text)
PM:MF:FF	Proximity to nearest mature forest following last fire
PM:MF:CY	Proximity to nearest mature forest in current landscape (2009)
PM:OG:FF	Proximity to old growth forest following last fire
PM:OG:CY	Proximity to nearest old growth forest in current landscape (2009)

Distances for PM metrics were calculated using the *'Near'* tool in Arc GIS and transformed using the natural logarithm. PM metrics were not calculated for plots greater than 110 years, since they would have been assigned a zero distance to nearest mature forest for current (2009) vegetation maps and no vegetation maps were available for the time they were last burnt. Likewise, the PM:MF:CY metric was not calculated for plots between 70 and 110 years, since these plots comprised forests containing mature eucalypt trees and would also have been assigned a zero distance to nearest mature forest.

5.3.4 Statistical Analysis

5.3.4.1 Assemblage response to temporal and spatial variation in landscape context

To analyse the response of assemblage variation to LCI metrics and site variables the absolute subplot cover data was imported into Primer 6.0 (Clarke and Gorley 2006). and square root transformed. Twenty-eight environmental variables considered most likely to have associations with wet eucalypt forest assemblage were selected from among available topographic, soil, climate and disturbance history data for all plots (chapter 4). These candidate variables were used in a distance based linear model (DistLM) using a step-wise regression procedure with R^2 as the selection criterion to rank candidates. From the results of the first DistLM analysis the highest ranking environmental variables were selected if they contributed at least 1.5% to the

accumulated R^2 (results not shown). The selected environmental variables were used as candidates for a second DistLM analysis using the 'Best' procedure with the Bayesian information criterion (BIC) score as the criterion for selecting the optimal combination of site variables for explaining assemblage variation; a lower BIC score indicates a better model. The ideal combination of environmental sites variables was defined as the group beyond which the addition of the next best variable contributed a net reduction in BIC of less than 2.0. Note the results of these analyses are described but not tabulated.

DistLM was also used to rank LCI metrics in terms of their association with assemblage variation, using a step-wise regression procedure with R^2 as the selection criterion. All those metrics contributing at least 1.5% to the accumulated R^2 were used as candidates together with optimal site variables to determine the combination of these LCI metrics and variables that provided the best explanation of assemblage variation, using the 'best procedure' in DistLM analysis and BIC as the selection criterion. Note the results of these analyses are described but not tabulated.

PERMANOVA models including the random effects of plots were also used to compare the strength of association between assemblage variation and each of the LCI metrics with and without the site variable forest age in which both LCI metrics and age were included as continuous covariates. Note that other than age, none of the other environmental site variables were included within the PERMANOVA modelling as covariates, since they obscured the relationship between assemblage response to spatial and temporal scale response of assemblage variation with LC. The reporting of *P*-values, which are based on permutations, are rounded to four decimal places.

5.3.4.2 Richness and cover responses for subgroups of plant species to temporal and spatial variation in LC

The association between the univariate response variables and LCI metrics and site variables was examined using mixed effect modelling specifying the random effects of plots, and specifying all other variables in the model as fixed effects. Mixed effect modelling was undertaken using gamlss 4.3−0 (Rigby and Stasinopoulos 2005;

Stasinopoulos and Rigby 2007; Stasinopoulos et al. 2014) within the R software platform (R Core Team 2014) (see chapter 3 for details). The response variables were each tested to determine the distribution family most appropriate for analysis based on BIC score. Visual inspection of residual diagnostic plots was also undertaken to check for residual normality. In some instances it was still necessary to transform the response variable. The cover of MFI species was square root transformed, while several of the richness metrics were relativised by dividing the recorded richness of the particular group of species or total richness by maximum richness plus one, to produce responses between zero and less than one.

Mature Forest Indicator (MFI) species were identified using indicator species analysis (see chapter 4 for details). Cover for this species group was determined by summing estimated subplot cover for each member of the group located in the subplot. To normalise richness of MFI species and epiphytic ferns, the number found in each subplot was divided by one plus the maximum richness of these species occurring in any of the subplots. Woody pioneer species were those woody plants not identified as MFI species and which were also not considered to be rainforest species (Jarman et al. 1984).

Only site variables selected as optimal for describing assemblage variation were tested in the mixed effect modelling. The Pearson correlation between each of the site variables most associated with assemblage variation and LCI metrics were calculated in R (Appendix 5.1 and Appendix 5.2).

To understand the relationships observed between the univariate response variables richness of MFI species in silvicultural forest and the PM metrics, plots were allocated into change in proximity classes based on whether they had increased or decreased their proximity to mature forest between when they were last burnt and 2009 (PMΔ). The PMΔ classes were: proximities changed by less than 30 m (PMΔ nil); proximities had increased by more than 30 m but less than 160 m (PMΔ increase); proximities had been more than 200 m away immediately after disturbance and had increased by more than 100 m (PMΔ large increase); or proximities had decreased by more than 30 m (PMΔ decrease). Correlations between these classes and fire frequency are presented in Appendix 5.1.

5.4 Results

5.4.1 Assemblage variation

5.4.1.1 Silvicultural regrowth forest

The group of environmental variables providing the best DistLM model of assemblage variation within silvicultural regrowth were soil nitrogen, rainfall in the driest period, pH, regrowth age, conductivity, maximum temperature and fire frequency in the previous century. Together this combination of site variables had a BIC score of 1839 (R^2 = 37%). In comparison the single best explanatory variable was calcium (BIC = 1890, R^2 = 11%). However calcium became redundant with the inclusion of additional variables (data not shown).

The model combining both environmental and LCI metrics that best explained variance in silvicultural regrowth assemblages included soil nitrogen, soil pH, regrowth age, conductivity, maximum temperature and LCI:FF:1k (BIC = 1839, R^2 = 36%). This model accounted for much the same variance with one less variable than the best site variable only model. The best combination models with fewer variables failed to include any LCI metrics.

When the best combination of environmental and LCI metrics were used as covariates in a PERMANOVA model including the random effects of sites, LCI:FF:1k was ranked third among the six covariates in its contribution to the components of variation (SS = 33746, pseudo-F = 5.17, *P* = 0.0001, square root of the components of variation = 11.68). Soil pH contributed the greatest explanation of variability among assemblages (SS = 62363, pseudo-F = 10.20, *P* = 0.0001, square root of the components of variation = 15.30) followed by silvicultural regrowth age (SS = 35560, pseudo-F = 5.44, *P* = 0.0001, square root of the components of variation = 11.20).

The comparative results for PERMANOVA models with each LCI metric confirmed that the metric with strongest association with silvicultural regrowth assemblages was LCI: FF:1k (Table 5–4). In the absence of other environmental variables almost all methods for calculating LCI were associated with silvicultural regrowth assemblage variation (Model 1 results, Table 5–4). However, assemblage variation appeared to be

more sensitive to differences in the temporal scale at which LCI metrics were calculated than whether LCI metrics were calculated at a 500 m or 1 km scale (Table 5–4).

Among the PM metrics the strongest association with silvicultural regrowth forest assemblage variation was obtained for the log-transformed distance to nearest old growth forest immediately after disturbance (PM:OG:FF) but the results for this metric were not significantly better than obtained for log transformed current distances to old growth (PM:OG:CY) (Table 5–4).

5.4.1.2 All regrowth forest

The environmental variables best explaining all regrowth assemblages (< 110 years since last disturbed) were calcium, age, soil nitrogen, rainfall in the driest period, maximum temperature, disturbance frequency in the last century, soil pH and conductivity (BIC = 3149, R^2 = 31%). The single best of these was calcium (BIC = 3224, R^2 = 8.3). The replacement of conductivity with PM:OG:FF only marginally improved the model strength (BIC = 3148, R^2 = 31%). None of the other LC metrics provided any greater improvement in model strength.

None of the DistLM models of regrowth assemblage variation that included only LC metrics were as strong as those including only site variables. PM:MF:CY was the strongest of the single LC metric models (BIC 3237, R^2 = 5.4%). The addition of PM:OG:CY was the metric that provided the most additional improvement in model strength (total BIC = 3230, R^2 = 8.3%). The best of the LCI metric models included LCI: FF:½k (BIC 3242, R^2 = 4.1%).

Among the PERMANOVA models of regrowth assemblage variation the strongest single covariate model contained PM:MF:FF, but it was only marginally better than PM:OG:FF. When age was included (model 2) PM:OG:FF provided a substantially stronger model for explaining remaining variation in assemblages (Table 5–4). LCI metrics provided similar results as those reported for silvicultural regrowth, the main difference being that when age was not included (model 1) the most best LCI metric was that calculated for landscapes following fire at the 500 m spatial scale (LCI:FF:½k) rather than the one kilometre spatial scale (Table 5–4).

Table 5-4. Forest assemblage variance explained by LCI and PM metrics when included as the only covariate in PERMANOVA model (Model 1) and when included with the covariate age in years (Model 2) for three subset of plots from three forest age classes. [See notes on next page.]

	Silvicultural regrowth < 50 years		**All regrowth forests < 110 years**		**Mature Forests >70**	
Metric:	Model 1 SS p-F (P)	Model 2 SS p-F (P)	Model 1 SS p-F (P)	Model 2 SS p-F (P)	Model 1 SS p-F (P)	Model 2 SS p-F (P)
LCI: BF: 1k	33760 3.4216 (0.0001)	30758 3.3248 (0.0009)	#21161 1.9637 (0.0339)	#21534 2.1563 (0.0171)	#47168 5.1541 (0.0001)	#23296 2.7553 (0.0044)
LCI: BF: ½k	25573 2.5489 (0.0073)	25602 2.7354 (0.0043)	#27416 2.5806 (0.0045)	#28144 2.8612 (0.0016)	#47951 5.2794 (0.0001)	**#24811** **2.9719** **(0.0017)**
LCI: FF:1k	**39521** **4.0531** **(0.0001)**	**37823** **4.1564** **(0.0002)**	42054 3.991 (0.0002)	**32027** **3.2519** **(0.0001)**	#48842 5.3621 (0.0001)	#20140 2.3678 (0.0115)
LCI: FF: ½k	35133 3.5765 (0.0003)	33727 3.6793 (0.0001)	**48870** **4.698** **(0.0001)**	31425 3.2125 (0.0006)	**#50747** **5.6066** **(0.0001)**	#22217 2.64 (0.0067)
LCI: CY: 1k	28299 2.8373 (0.0026)	24023 2.5623 (0.007)	22961 2.1441 (0.0182)	22168 2.2321 (0.0145)	11232 1.1436 (0.3342)	12897 1.5005 (0.1457)
LCI: CY: ½k	21107 2.103 (0.0327)	20823 2.2232 (0.0185)	20767 1.9495 (0.0364)	14667 1.477 (0.1437)	8565 0.8731 (0.5726)	8937.1 1.0367 (0.4227)
PM:OG:FF	23873 2.4504 (0.0103)	20167 2.2094 (0.0224)	54930 5.7669 (0.0001)	**45576** **5.1209** **(0.0001)**		
PM:MF:FF	05549 0.5376 (0.829)	04528 0.46915 (0.8836)	**60044** **5.8375** **(0.0001)**	23609 2.3939 (0.0108)		
PM:OG:CY	22377 2.2542 (0.0207)	19045 2.0423 (0.0324)	24556 2.4770 (0.0001)	18417 1.9934 (0.0294)		
PM:MF:CY	10646 1.0306 (0.4322)	10719 1.1107 (0.3701)	n.a.	n.a.		

Table 5–4 notes

*****All PERMANOVA models included the random effect of plots.**

SS = sums of squares; p-F = pseudo F-score; *P* = probability based on permutations, rounded to four decimal places.

In Model 2 of silvicultural regrowth < 50 years, the total variance of explained was 626690 and for Model 2 age had an SS of 41885 with a p-F > 4.3319 and < 4.5749 and *P* = 0.0001.

In Model 1 and Model 2 of all regrowth < 110 years, the total variance explained was 1147700 and for Model 2 age had an SS of 73999 with a Pseudo-F of 7.3519 and a *P* = 0.0001.

In Model 1 and Model 2 of mature forests > 70 years, the total variance explained was 742600 and the residual was 193930 and for Model 2 age had an SS of 73405 with a p-F of 8.6244 and a *P* = 0.0001.

Note the SS for the random effects of plots was negatively associated with SS for LC metrics.

When LCI metrics calculations require vegetation mapping prior to 1924, they were instead calculated from the 1924 vegetation map as per Table 5–2.

^ When LCI metrics calculations require vegetation maps after to 2009, they were instead calculated from the 2009 vegetation map as per Table 5–2.

5.4.1.3 Assemblage variation in mature forest

The environmental site variables contributing to the best DistLM model for explaining the variation in forest with mature eucalypts were age class, nitrogen, mean annual temperature, annual rainfall and calcium (BIC = 2120.7, R^2 = 28%). There were no landscape metrics that led to any further reduction in BIC although the addition of LCI: FF: 1k provided the greatest additional contribution to accumulated R^2 (~1%). The best single variable model comprised forest age class (BIC = 2155, R^2 = 9.9%). The best DistLM model including only LCI metrics included just LCI:FF:½k (BIC = 2164.6, R^2 = 8.6%).

The results of PERMANOVA models for mature forest plots demonstrated again that the levels of association were more strongly affected by the temporal scale than the spatial scale of the LCI metric. For PERMANOVA models 1 the LCI metric associated most strongly with assemblage variation was LCI:FF:½k but LCI:FF:1k was only marginally weaker. However, when forest age class was accounted for (Model 2) the metric contributing the greatest strength to the model was LCI:BF:½k although it was only marginally stronger than other historical LCI metrics (Table 5–4). It is noteworthy that there was no evidence of any relationship between the mature forest assemblages and the CY LCI metrics (Table 5–4).

5.4.2 Mature forest indicator species cover in silvicultural regrowth forest

Mixed effect models of the untransformed MFI species cover response accounted for the random effects of plots and using a beta distribution for the analysis, provided evidence that the LCI:FF:½k metric provided the strongest model of all LC metrics (Data not shown). For the square root transformed response the residuals were most normal when the data was analysed using a normal distribution model. Among models of the square root transformed MFI species cover response, PM:MF:CY provided a slightly stronger model than any including LCI metrics (Table 5–5). The LCI metric most associated with the square root transformed MFI cover response was LCI:BF:1k (Table 5–5). However, this model was only a marginally better than the model with LCI:FF:½k (difference in BIC, i.e. ΔBIC ~0.5, Table 5–5).

When site variables were included in the modelling for both square root transformed and untransformed MFI species cover data (specifying either beta or normal family distribution), the LCI metric contributing to the greatest improvement in model strength in all cases was LCI:FF:½k (Table 5–6), though the results for LCI:FF:1k were only marginally weaker (data not shown). The site variables contributing the greatest improvement in model strength were silvicultural forest age, fire frequency in the last century and mean rainfall in the driest week (Table 5–6). The substitution of maximum temperature of the warmest period for rainfall also provided only a marginally weaker model (△BIC <0.1). The increase in BIC resulting from the omission of the LCI metric from the model was greater than that which resulted from each of the other three site variables for the untransformed cover response (△BIC = 6.2 family=Beta, △BIC = 8.5, family=Normal, results not shown). However the contribution of this LCI metric was weaker relative to the site variables for the square root transformed MFI species cover response (Table 5–6). The inclusion of terms in the Sigma model (variance) did not improve the overall model strength but results did demonstrate that for high LCI scores there was a greater variance in the untransformed cover of MFI species (t = 4.53, $P < 0.0001$, family = normal).

Table 5-5. Strength of association between square root cover of mature forest indicator within silvicultural regrowth forests and each LC metric using gamlss mixed effect modelling (normal family**)**

Metric:	Rank	BIC	t-value	*P*-value
LCI: BF: ½k	4	1005.1	3.54	0.0005
LCI: FF: ½k	**3**	**1004.2**	**4.27**	**0.0000**
LCI: CY: ½k	7	1006.0	3.13	0.0020
LCI: BF: 1k	**2**	**1003.7**	**4.41**	**0.0000**
LCI: FF: 1k	5	1005.3	4.08	0.0001
LCI: CY: 1k	8	1006.6	2.59	0.0102
PM:OG:FF	10	1007.6	-2.94	0.0036
PM:MF:FF	9	1007.4	-2.10	0.0368
PM:OG:CY	6	1005.9	-2.68	0.0080
PM:MF:CY	**1**	**1003.1**	**-3.30**	**0.0011**
No metric (Null model)		1008.1		

The best model including both PM metrics and site variables included PM:MF:CY, and provided a marginally stronger result than the model within the best LCI metric. The best overall model developed included both LCI:FF:½k and PM:MF:CY (Table 5–7). The same site metrics were important in all cases and there was no evidence for an interaction effect on the response for any of the predictors tested.

The model predictions (after excluding unexplained random differences between plots) demonstrate that the square root of MFI species cover is predicted to be less than the overall mean for the sampled range when proximity to mature forest is greater than 150 m (ln150 = 5); LCI scores are less than 4, silvicultural regrowth forest is less than 30 years old, mean rainfall for the driest week is less than 17 mm (or mean maximum temperatures in the warmest week are more than 20^{o}C) or when forests are burnt more than once in the century (Figure 5–1).

Table 5-6. Best mixed effect model for square root cover of mature forest indicator species in silvicultural regrowth forest including LCI metric (normal family, BIC = 992.4)

Model term:	Mu coefficient	Std dev	t-value	*P*-value	△ in BIC without term
Intercept	-13.7559	3.2974	-4.17	0.0000	
LCI:FF:½k	0.6424	0.2271	2.83	0.0052	3.8
Regrowth forest age (years)	0.0709	0.0188	3.76	0.0002	5.8
Fire Frequency (2)	-1.2563	0.5085	-2.47	0.0172	3.2
Mean rainfall in driest period (mm)	0.5752	0.1881	3.06	0.0025	4.7
all model terms:					15.7
Intercept only (Null model) BIC: 1008.1					

Table 5-7. Best mixed effect model for square root cover of mature forest indicator species in silvicultural regrowth forest including any LC metrics (normal family, BIC = 988.0)

Model term:	Mu coefficient	Std dev	t-value	*P*-value	△ in BIC without term
Intercept	-11.7292	3.2785	-3.58	0.0004	
PM:MF:CY	-0.3098	0.1272	-2.44	0.0158	4.4
LCI:FF:½k	0.5628	0.2212	2.54	0.0118	3.1
Regrowth forest age (years)	0.0772	0.0183	4.22	0.0000	7.7
Fire Frequency (2)	-1.0148	0.4988	-2.03	0.0476	2.4
Mean rainfall in driest period (mm)	0.5448	0.1813	3.01	0.0030	4.9
all model terms:					20.1
Intercept only (Null model) BIC: 1008.1					

5.4.3 Total richness within silvicultural regrowth forest

Mixed effect modelling demonstrated that the PM metrics provided stronger models than the LCI metrics (Table 5–8). The PM metric with the strongest association was PM:MF:CY, while among the LCI metrics it was LCI:CY:1k that provided the strongest model (Table 5–8).

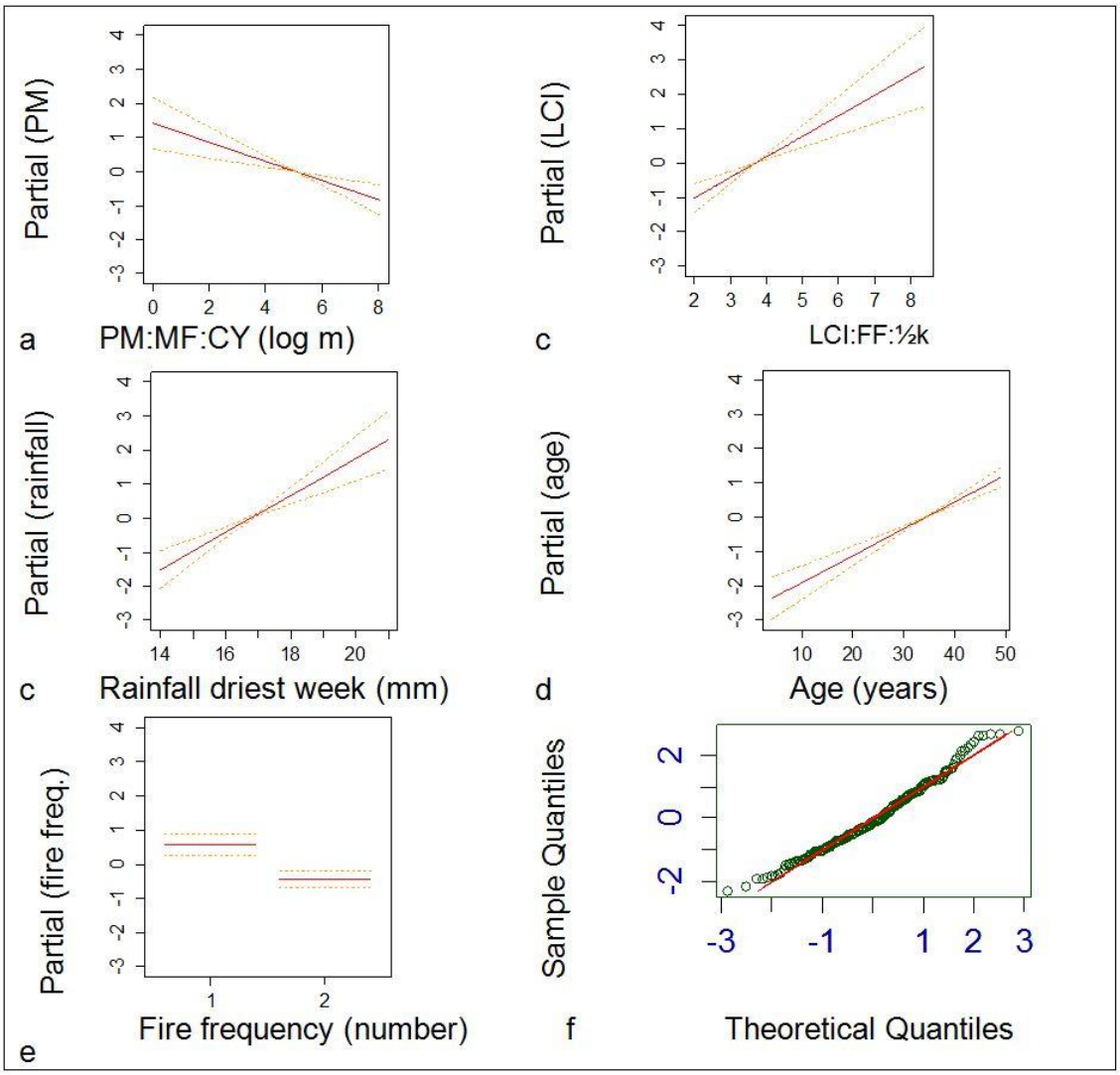


Figure 5-1. Partial MFI species cover response in silvicultural regrowth forest for each predictor (a to e) together with diagnostic residual plots (f) for generalised linear model, excluding the random effects of site differences.

Plots (a to e) show fitted line (with standard error) for partial residuals (i.e. sum of the residual and predictor terms) for each predictor term in best generalised linear model for square root transformed MFI species cover in silvicultural regrowth forest (family=normal, BIC=1025.0).

The best model developed with a combination of PM metrics and site variables included the first and second order polynomial of the PM:MF:CY together with first and second order polynomial of the square root transformed soil nitrogen (Table 5–9).

The best model using LCI metrics and site variables included LCI:FF:1k and the square root transformed soil nitrogen, but this model was substantially weaker than the model developed with the PM metric (Δ BIC = 16.5, data not shown). A slightly

better model included both the PM:MF:CY and LCI:FF:1k metrics with square root soil nitrogen (BIC = 1305.6, data not shown) but the marginal improvement in BIC did not justify the additional model complexity (Δ BIC < 2).

The partial plots for each of the model predictor variables demonstrate that within the sampled range of silvicultural forests total species richness is likely to be below average when the nearest mature forests are further away than 150 m and nitrogen exceeds 4.0 mg per litre of soil (Figure 5–2). When the LCI:FF:½k was included in the model, values below 4 were predicted to be associated with a below average response in total species richness (data not shown).

5.4.4 Richness of mature forest indicator species within silvicultural regrowth forest

Comparisons among metrics included within mixed effect models provided evidence that when taking into account the random effects of plots, the metric most strongly associated with relative richness of MFI species was PM:MF:CY, although only marginally stronger than PM:OG:CY. Among the LCI metrics the strongest model included LCI:FF:1k (Table 5–10).

Table 5-8. Strength of association between total species richness for a selection of LC metrics within silvicultural regrowth forests using gamlss mixed effect modelling (normal family).

Metric:	Rank	BIC	t-value	*P*-value
LCI: BF: ½k	ns	1346.6	1.58	0.1161
LCI: FF: ½k	ns	1345.4	1.93	0.0552
LCI: CY: ½k	ns	1345.5	1.94	0.0534
LCI: BF: 1k	ns	1346.2	1.71	0.0888
LCI: FF: 1k	6	1343.5	2.48	0.0141
LCI: CY: 1k	5	1342.8	2.7	0.0076
PM:OG:FF	3	1337.2	-3.72	0.0003
PM:MF:FF	4	1340.9	-3.08	0.0023
PM:OG:CY	1	1336.1	-3.90	0.0001
PM:MF:CY	2	1336.6	-3.90	0.0001
No metric (Null model)		1348.5		

Table 5-9. Results of best Gamlss mixed effect model for total species richness in silvicultural regrowth forest including both LC metrics and site variables (normal family, BIC = 1306.7).

Model term:	Mu coefficient	Std dev	t-value	*P*-value	△ in BIC without term
Intercept	-0.0016	0.2788	-0.01	0.9955	
PM:mf:CY first order polynomial	-23.1963	4.3958	-5.28	0.0000	25.4
PM:mf:CY second order polynomial	-9.0346	4.3581	-2.07	0.0395	6.6
Sqrt Nitrogen, first order polynomial	-15.3106	4.4210	-3.46	0.0007	12.2
Sqrt Nitrogen, second order polynomial	-12.6869	4.4413	-2.86	0.0048	11.6
all model terms:					36.2
Intercept only (Null model) BIC = 1348.5					

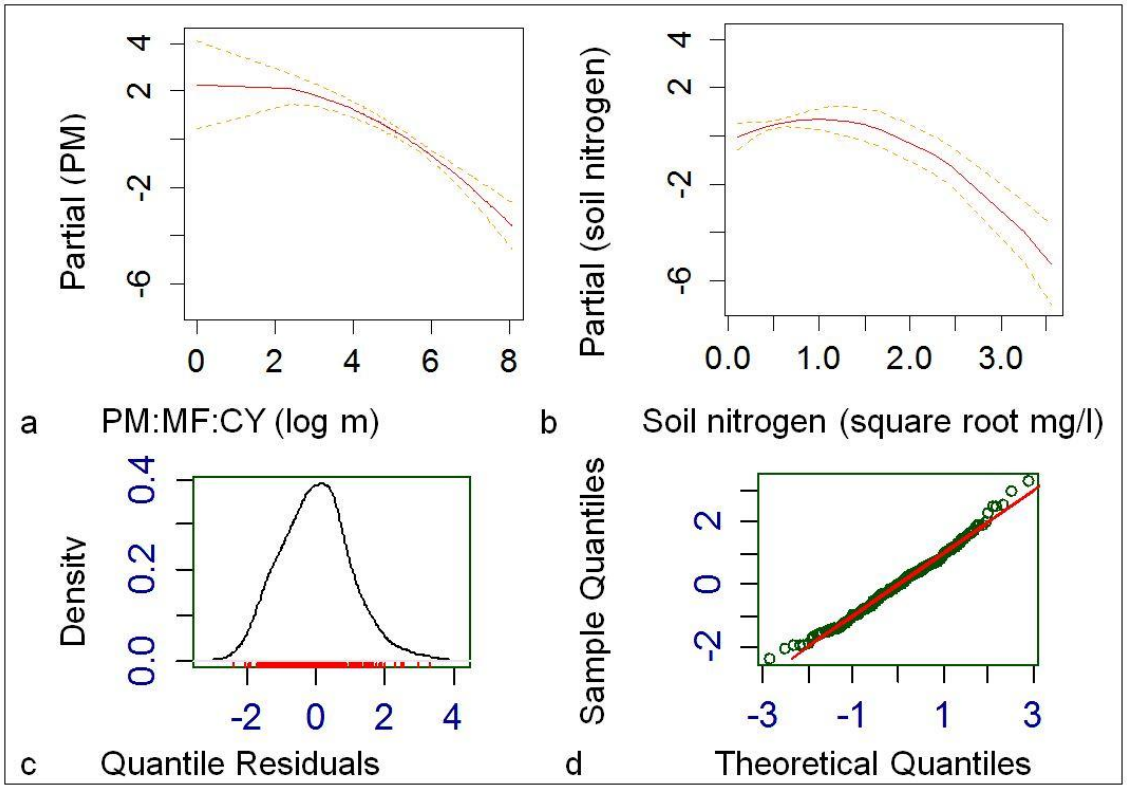


Figure 5-2. Fitted line (with standard error) for partial plots for each predictor term (a & b) in best generalised linear model for total species richness in silvicultural regrowth forest (family=normal, BIC=1263.8). (c & d) Diagnostic residual plots (c & d).

Table 5-10. Strength of association of relative richness of MFI species within silvicultural regrowth forests with a selection of LC metrics using mixed effect modelling (normal family).

Metric:	Rank	BIC	t-value	*P*-value
LCI: BF: ½k	7	-207.7	3.65	0.0003
LCI: FF: ½k	6	-208.4	3.32	0.0011
LCI: CY: ½k	8	-207.2	2.84	0.0049
LCI: BF: 1k	4	-211.5	4.91	0.0000
LCI: FF: 1k	9	-206.8	3.09	0.0023
LCI: CY: 1k	12	-205.3	2.22	0.0276
PM: FF: OG	3	-212.8	-3.82	0.0002
PM:FF:MF	5	-209.4	-2.65	0.0086
PM:CY:OG	1	-216.6	-3.92	0.0001
PM:CY:MF	2	-215.2	-3.99	0.0001
No metric (Null model)		-203.4		

The best mixed effect model included the LC metric PM:MF:CY and four site variables: age, fire frequency, precipitation in driest week and soil conductivity. The partial plots for the generalised linear model of fixed effects of this variable group predict that richness of MFI species will be below average in forests less than 30 years old, those disturbed more than once in the previous century, those with rainfall under 17 mm in the driest week, those with soil conductivities of less than 80, and those more than 150 m from the mature forest edge (Table 5–11).

To examine the effect of changing proximities the factor 'change in proximity to mature forest' (PMΔ) was added to the best mixed effect model. With the addition of this factor fire frequency became redundant, demonstrating a correlation between PMΔ and fire frequency (see Appendix 5.1 for more details). Without the variable fire frequency there was weak evidence that there was higher than expected richness of MFI species in class PMΔdecrease (n = 3 plots) compared with plots in class PMΔlarge increase(n = 9 plots; t = 1.96, $P = 0.05$, data not shown). Differences among other class pairs did not reach significance at the alpha level 0.05.

Table 5-11. Results of best mixed effect model for relative richness of mature forest indicator species in silvicultural regrowth forest including both LC metrics and site variables (normal family, BIC = -246.1).

Model term:	Mu coefficient	Std dev	t-value	*P*-value	△ in BIC without term
Intercept	-0.9459	0.2383	-3.97	0.0001	
PM:MF:CY	-0.0260	0.0092	-2.84	0.0051	7.9
Age of silvicultural regrowth (years)	0.0058	0.0013	4.62	0.0000	12.2
Fire frequency (2:)	-0.0699	0.0344	-2.03	0.0478	2.7
Mean rainfall in driest week (mm)	0.0547	0.0121	4.53	0.0000	11.5
Soil conductivity, first order polynomial	0.6380	0.2175	2.93	0.0038	2.2
Soil conductivity, second order polynomial	-0.6080	0.1727	-3.52	0.0005	12.9
all model terms:					42.7
Intercept only (Null model) BIC = -203.4					

Table 5-12. Strength of association of relative richness of epiphytic fern species within silvicultural regrowth forests with a selection of LC metrics using mixed effect modelling (Poisson family).

Metric:	Rank	BIC	t-value	*P*-value
LCI: BF: ½k	2	741.5	2.16	0.0319
LCI: FF: ½k	ns	744.7	0.55	0.5853
LCI: CY: ½k	ns	744.0	1.20	0.2336
LCI: BF: 1k	1	732.7	4.07	0.0001
LCI: FF: 1k	ns	744.8	0.38	0.7067
LCI: CY: 1k	ns	744.9	0.13	0.8954
PM:OG:FF	ns	743.1	-1.54	0.1248
PM:MF:FF	ns	743.4	-1.31	0.1922
PM:OG:CY	ns	743.1	-1.48	0.1416
PM:MF:CY	ns	743.2	-1.55	0.1240
No metric (Null model)		744.9		

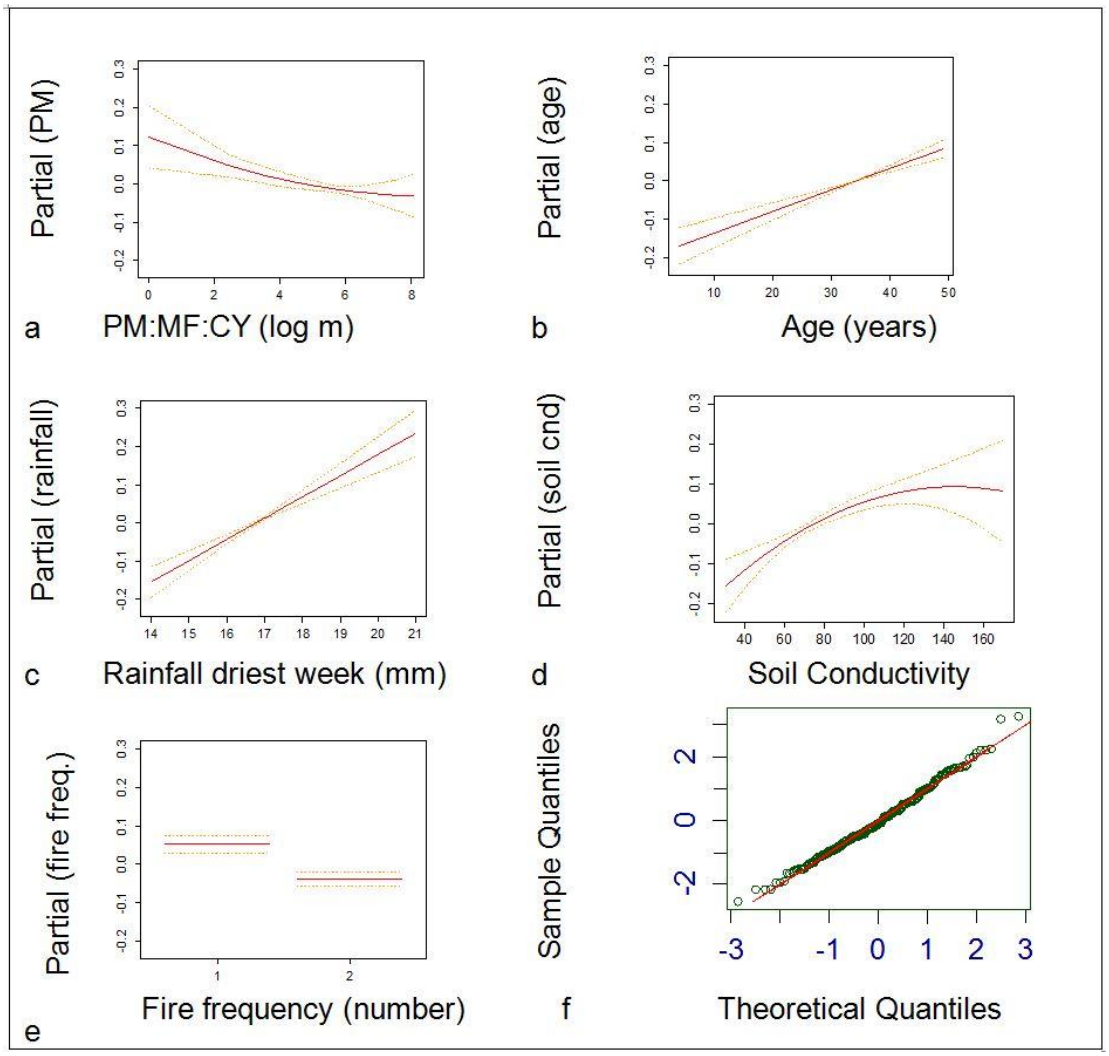


Figure 5-3. Fitted line (with standard error) for partial residuals (i.e. sum of the residual and predictor terms) for each predictor term (a to e) in best generalised linear model for relative richness of mature forest indicator species in silvicultural regrowth forest (family=normal, BIC = -241.4) together with diagnostic residual plots for predicted model without random effects of plots accounted for (f).

5.4.5 Richness of epiphytic ferns species in silvicultural regrowth forest

Comparisons among metrics within mixed effect models provided evidence that it was LCI:BF:1k metric that was the most strongly associated with epiphytic fern richness with none of the other temporal scale LCI metrics and none of the PM metrics being significantly associated with this response (Table 5–12).

The only LC metric to provide additional strength to the best mixed effect model when site variables were included was PM:OG:CY. The site variables included in the model were regrowth age, disturbance frequency, mean rainfall in the driest week, soil pH and conductivity. Within the sampled range, richness of epiphytic ferns was reduced below mean values when proximities to old growth forest were greater than about 150 m, forests were less than 30 years in age, mean rainfall was under 17 mm in the driest week, soil pH was under 5.0, and soil conductivities were less than 80 units (Table 5–13, Figure 5–4).

Table 5-13. Results of best mixed effect model for richness of epiphytic fern species in silvicultural regrowth forest including both LC metrics and site variables (Poisson family, BIC = 744.9).

Model term:	Mu coefficient	Std dev	t-value	*P*-value	△ in BIC without term
Intercept	-14.0832	3.1415	-4.48	0.0000	
PM:OG:CY	-0.2012	0.0982	-2.05	0.0418	3.1
Age of silvicultural regrowth (years)	1.4099	0.2519	5.60	0.0000	55.1
Mean rainfall in driest week (mm)	0.2220	0.1114	1.99	0.0477	4.1
Soil pH	0.4765	0.2036	2.34	0.0203	4.4
Soil conductivity, first order polynomial	4.8189	2.0982	2.30	0.0227	0.1
Soil conductivity, second order polynomial	-3.5880	1.1677	-3.07	0.0024	8.1
all model terms:					65.1
Intercept only (Null model) BIC: 689.8					

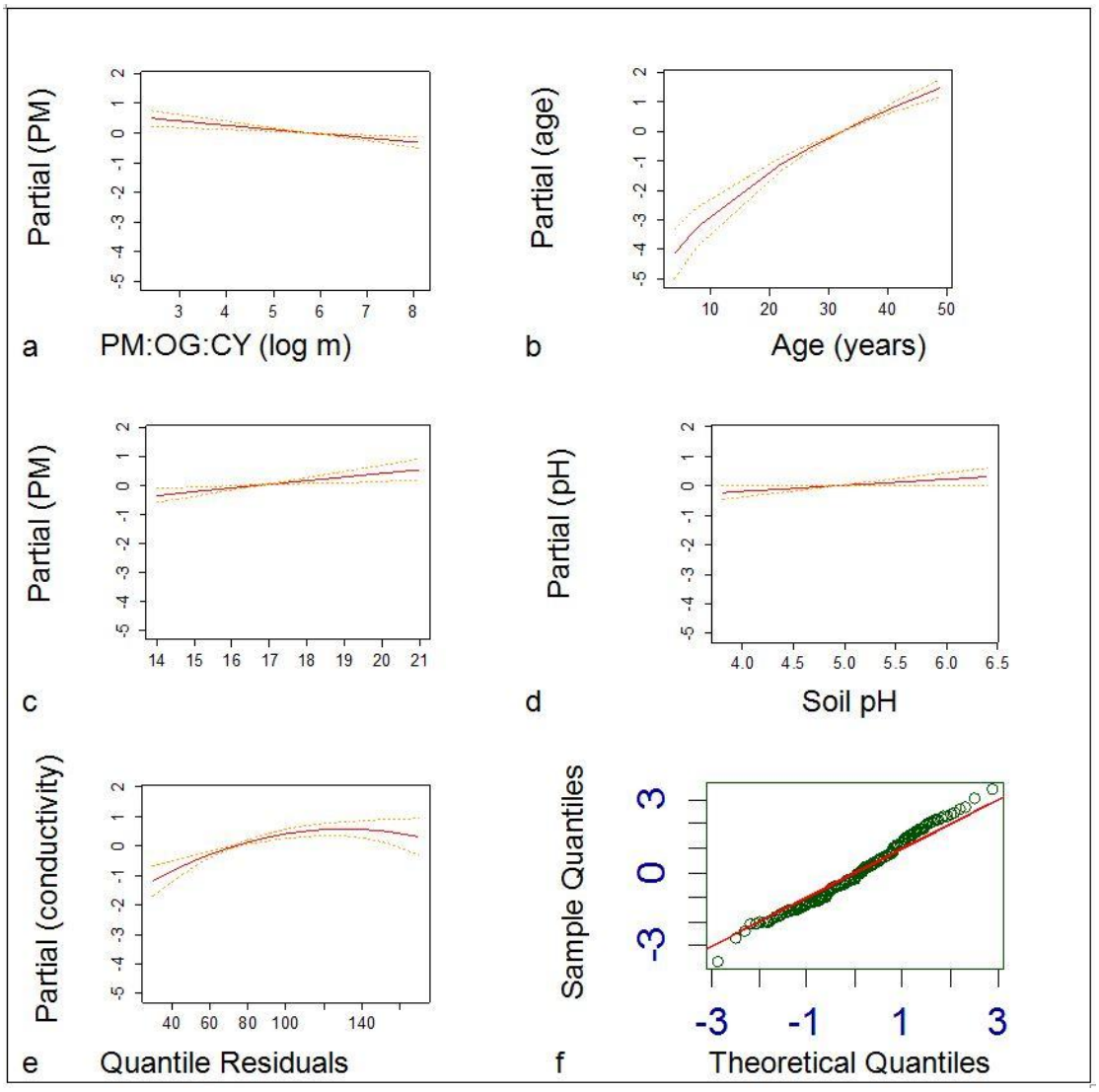


Figure 5-4. Fitted line (with standard error) for partial residuals (i.e. sum of the residual and predictor terms) for each predictor term (a to e) in best generalised linear model of epiphytic fern species richness in silvicultural regrowth forest (family = Poisson, BIC = 721.1) together with diagnostic residual plot for predicted model without accounting for random effects of plots (f).

5.4.6 Richness of woody pioneer species in silvicultural regrowth forest

Comparisons among the mixed effect models for each of the LC metrics demonstrated that the only metric associated with the richness of woody pioneer species were the LCI metrics calculated for landscapes prior to the last disturbance. The association was weakly negative, improving the BIC by only 2 units compared with an intercept only model (Table 5–14). With the inclusion of site variables in a full mixed effect

model, none of the LC metrics were able to add additional strength to the model. This response variable had a strong negative association with silvicultural forest age, rainfall and the intermediate range in soil conductivity (Table 5–15).

Table 5-14. Strength of association of richness of woody pioneer species within silvicultural regrowth forests with a selection of LC metrics using mixed effect modelling (normal family).

Metric:	Rank	BIC	t-value	*P*-value
LCI: BF: ½k	2	973.5	-2.45	0.0152
LCI: FF: ½k	ns	974.5	-1.92	0.0569
LCI: CY: ½k	ns	973.4	-1.90	0.0593
LCI: BF: 1k	1	973.2	-2.84	0.0050
LCI: FF: 1k	ns	975.5	-1.13	0.2585
LCI: CY: 1k	ns	975.3	-0.65	0.5144
PM:FF:OG	ns	974.4	1.05	0.2943
PM:FF:MF	ns	975.5	-0.03	0.9742
PM:CY:OG	ns	974.8	0.77	0.4450
PM:CY:MF	ns	974.3	0.84	0.4016
No metric (Null model)		744.9		

Table 5-15. Results of best mixed effect model for richness of woody pioneer species in silvicultural regrowth forest including both LC metrics and site variables (normal family, BIC = 959.3).

Model term:	Mu coefficient	Std dev	t-value	*P*-value	△ in BIC without term
Intercept	12.7609	2.8062	4.55	0.0000	
Age of silvicultural regrowth (years)	-0.0772	0.0176	4.38	0.0000	7.3
Mean rainfall in driest week (mm)	-0.6033	0.1538	3.92	0.0001	5.9
Soil conductivity, first order polynomial	-6.5444	2.8760	2.28	0.0240	-1.1
Soil conductivity, second order polynomial	7.6616	2.1683	3.53	0.0005	9.2
all model terms:					16.2
Intercept only (Null model) BIC: 975.5					

5.4.7 Total species richness in mature forest

Mixed effect modelling of total species richness demonstrated that none of the LCI metrics were associated with total species richness in mature forests (Table 5–16).When modelling included site variables, LCI metrics also failed to contribute any additional strength to the models. The strongest model included mean annual temperature, soil pH and a four level factor (FA class) in which plots were grouped according their fire frequency and age class (old growth sites; 60-80 year old sites burnt once since 1897; 60-80 year old sites burnt twice since 1897, and 80-110 years burnt once since 1897). Residuals were best normalised using the Box-Cox transform distribution family (Figure 5–5). Species richness increased with increasing soil alkalinity and decreased with mean annual temperatures. Predictions for species richness were lowest for forests burnt twice in the last century (FA:a), greatest for plots burnt only once prior to 1934 (FA:c) and intermediate for both the old growth forests (FA:d) and forests burnt only once last century but more recently than 1930 (FA:b). Among the four FA classes only class FA:a could be distinguished as having significantly lower richness levels than FA:c (Table 5–17). The difference in richness between all other pairs of FA classes could not be distinguished from chance variation at the alpha level of 0.05.

5.4.8 Richness of mature forest indicator species in mature forest

Four LCI metrics were associated weakly with relative richness of MFI species in mature forests, the strongest of which was LCI: FF: ½k (Table 5–18). When mixed effect models included site variables none of the LCI metrics provided additional strength to the model. Site variables best predicting this response included FA class and mean annual rainfall. MFI species richness was predicted to increase with rainfall and to be highest in old growth forests and lowest for forest forests burnt twice in the previous century (Table 5–19).

Table 5-16. Strength of association of total richness within all mature forests with a selection of LC metrics using mixed effect modelling (Box-Cox transform family).

Metric:	Rank	BIC	t-value	*P*-value
LCI: BF: ½k	ns	1635.9	0.14	0.8915
LCI: FY: ½k	ns	1636.0	-0.14	0.8855
LCI: CY: ½k	ns	1635.6	0.80	0.4274
LCI: BF: 1k	ns	1635.6	0.49	0.6230
LCI: FF: 1k	ns	1635.8	0.33	0.7420
LCI: CY: 1k	ns	1635.9	0.46	0.6484
No metric (Null model)		1636.0		

Table 5-17. Results of best mixed effect model for richness of woody pioneer species in silvicultural regrowth forest including both LC metrics and site variables (Box-Cox transform family, BIC = 1602.7)

Model term:	Mu coefficient	Std dev	t-value	*P*-value	△ in BIC without term
Intercept [FA:a:2 fires since 1898]	12.7609	2.8062	4.55	0.0000	
FA:d: 0 fires since 1898(old growth)	1.3186	0.9120	1.45	0.1543	10.4
FA:c:1 fire between 1898 and 1930	2.7220	1.1958	2.28	0.0271	
FA:b:1 fire after 1930	1.7534	0.9837	1.78	0.0806	
Mean annual temperature	-0.1448	0.0563	-2.57	0.0131	8.3
Soil pH	1.8176	0.5938	3.06	0.0025	13.2
all model terms:					16.2
Intercept only (Null model) BIC: 1636.0					**33.3**

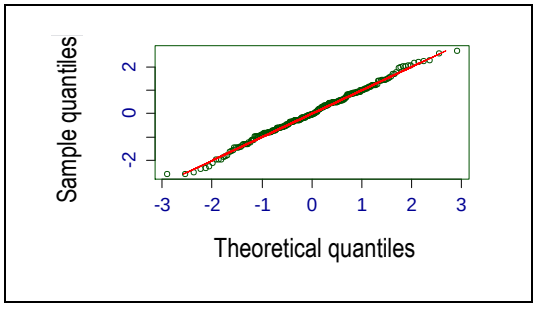


Figure 5-5. Diagnostic QQ plots of residuals for gamlss mixed effect model of total species richness in mature forest (family BCT, see Table 5–17 for model details)

Table 5-18. Strength of association of richness of mature forest indicator species in mature forest with a selection of LC metrics using mixed effect modelling (normal family).

Metric:	Rank	BIC	t-value	*P*-value
LCI: BF: ½k	3	-202.6	2.84	0.0049
LCI: FF: ½k	1	-203.3	3.12	0.0020
LCI: CY: ½k	ns	-201.8	0.23	0.8173
LCI: BF: 1k	4	-202.4	2.77	0.0061
LCI: FF: 1k	2	-202.7	2.96	0.0035
LCI: CY: 1k	ns	-201.8	0.05	0.9600
No metric (Null model)		-201.8		

Table 5-19. Results of best mixed effect model for richness of mature forest indicator species in mature forest including both LC metrics and site variables (normal family, BIC = 201.8).

Model term:	Mu coefficient	Std dev	t-value	*P*-value	△ in BIC without term
Intercept [FA:d:2 fires since 1898]	-0.8213	0.1983	-4.14	0.0000	
FA:d 0 fires since 1898, old growth	0.3578	0.0699	5.12	0.0000	5.9
FA:c 1 fire between 1898 and 1930	0.2908	0.0815	3.57	0.0008	
FA:b 1 fire after 1930	0.2213	0.0732	3.02	0.0039	
Mean annual rainfall	0.0004	0.0001	2.98	0.0044	2.4
all model terms:					**8.0**
Intercept only (Null model) BIC: 209.8					

5.5 Discussion

5.5.1 Floristic response to landscape context in silvicultural regrowth of wet eucalypt forest

The results of the present study add to the evidence from the previous two chapters that LC is associated with floristic variation within native wet eucalypt forest. The study has established that less than average covers and richness of MFI species were present in silvicultural plots more than 150 m from mature forest or in landscapes with a LCI score of less than 4.0. This adds support to the findings of other regional studies that surrounding landscapes may influence forests in a range of ecosystem types including: the Amazonian rainforest, Brazilian temperate rainforest, Argentine Chaco dry forest, western European temperate oak woodlands, and other temperate forests in Spain (Grau 2004; Laurance et al. 2006; Vellend et al. 2006; Gasparri and Grau 2009; Metzger et al. 2009; Martin-Queller and Saura 2013; Rigueira et al. 2013).

In particular, the current study demonstrated that the floristic composition in all forest age classes was associated most closely with the LCI metrics calculated for the years immediately after disturbance compared with current year LCI metrics, and that the temporal scale of calculation affected the strength of association more than the difference between calculating the metric for a landscape of 500 m compared with 1000 m radius. Nevertheless, assemblages in regrowth forests were associated weakly with current LC metrics. There was no evidence that mature forest assemblages were associated with current year LCI metrics. There was also strong evidence that forest assemblages were more stronger determined by site environment and disturbance history than by LC influence. Nevertheless, the results from the analysis of assemblage data were consistent with the hypothesis that wet eucalypt forest communities and their successional trajectory are more strongly influence by their LC at the time of disturbance. This suggests that responses of plants to 'temporal spatial connectivity' is not linear.

Despite the relatively strong association between mature forest assemblages and historical LC metrics with PERMANOVA, the results of mixed effect models demonstrated only a weak associations between MFI species richness in mature

forests and the historical LCI metrics, and found no evidence at all for an association between total richness in mature forests and LC metrics. An interpretation of these results is that with increased time following disturbance species richness in wet eucalypt forest gradually reaches an equilibrium which is determined by the site environment and forest age rather than the LC, at least in areas beyond the influence of forest edges, and disturbance gaps. A slow turnover in species in response to LC may still occur as succession progresses but this may not be evident in the richness data.

Despite the consistently stronger association between silvicultural regrowth forest assemblages and historical LCI metrics the results for other responses in silvicultural regrowth forest using mixed effect models provided less consistent results, and only equivocal support for the hypothesis. While cover of MFI species was consistently more strongly associated with historical LCI metrics, total richness, was consistently more strongly associated with the current year proximity metrics. Models of richness demonstrated a non-linear relationship with proximity to mature forest suggesting that it is maximised at intermediate distances from mature forest. At face value this result suggests that LC influence continues to be important as silvicultural forest ages, demonstrating that species colonization may continue to occur in these forests for at least 50 years. However there are issues with the proximity data (see section 5.5.2) that make interpretation of this results uncertain.

There was some evidence from the mixed effect models without environmental site variables that richness of MFI species was more strongly associated with LCI metrics calculated for landscapes following fire, but the richness of epiphytic ferns and the richness of woody pioneer species were both more strongly associated with LCI metrics developed for landscapes prior to the fire year. However when site history and environmental variables were included in the models for richness of MFI species and epiphytic fern species, it was the proximity metrics for the current year landscape that explained additional variation. The historical LCI metrics were excluded from full models for both the responses of richness of MFI species and richness of epiphytic fern species and none of the LCI metrics were included in full models developed for the richness of woody pioneer species. This suggests that it is mainly the woody subgroup of MFI species that is driving the response of these forest communities to

the LC metrics, rather than the epiphytic ferns or woody pioneer species. The inconsistency of these results is given greater consideration in section 5.5.2.

The significantly better performance of historical LCI metrics compared with current LCI metrics for most of the responses tested in the current study provided evidence that vegetation recovery and post-disturbance succession may be influenced by the historical landscapes of wet forest patches. However, the results also show that silvicultural floristic responses are also associated with LCI metrics derived from current landscapes. This is likely to be at least partly explained by the fact that for close to half of the silvicultural plots, nearby landscapes have changed little since the sampled forests were last burnt, and the LCI metrics are strongly auto-correlated between spatial scales.

Previous studies aiming to associate plant species responses and traits to historical landscape patterns, including historical patch sizes, have not, to my knowledge, attempted to relate the response to the landscapes present at the time the patch was last disturbed. Instead, they have simply compared current patterns with known historical landscape patterns at fixed points back in time (e.g. Vellend et al. 2006; Gasparri and Grau 2009; Metzger et al. 2009; Kimberley et al. 2015). Yet in many ecosystems it is stochastic disturbance events that are likely to be associated with atypical peaks in mortality and colonization, providing a greater opportunity for species turn-over, which could well be influenced by LC.

While opportunities for change may be more evident following timber harvesting in ecosystems not typically subject to extreme disturbance, it may be that the rate of colonization is determined more by the traits of the local species pool and whether the natural disturbance rate that these species are adapted to. For example in a study of plantations of oak trees located adjacent to native woodland patches, the richness of native woodland species in the plantation continuously increased with its age and had reached a similar richness as adjacent forest after 80 years (Brunet 2004, 2007). From this example and the general theories of succession it is clear that the temporal scale for colonization following disturbance varies greatly between species and may depend on plant characteristics such as competitive capacity and tolerance of post-disturbance conditions (Pulsford et al. 2016). For the same reasons it is likely that the long lag

time between the arrival of alien species in the landscape and their colonization of native forest habitats is a result not of a particular resistance to invasion but to their generally low rate of natural disturbance and the greater longevity of the dominant species giving rise to a slower rates of species colonization generally (Essl et al. 2011). The long lag between arrival of alien species and their eventual naturalization in native vegetation has led to complacency about managing alien species. In New Zealand, where the native forest ecosystems have a low rate of natural disturbance, the increasing rate of plant species naturalization has been linked to increased anthropogenic disturbance (Kelly and Sullivan 2010). The naturalized flora now equals the native flora in New Zealand and it is likely that extinction rates of native species will increase as more alien species become naturalized (Kelly and Sullivan 2010).

If the results of the present study were to support the initial hypothesis, which was that the landscapes around disturbance patches have a greater influence on the distribution of species at the time of disturbance than later landscape patterns then I would have expected the historical PM metrics to provide a stronger association with the responses than the current PM metrics. While the general assemblages of silvicultural forests and all regrowth forests less than 110 years were more strongly associated with historical PM metrics, the differences in model strength were not sufficient to provide evidence that historical proximities provided a significantly better explanation of the data than current proximities. Furthermore, the models provided evidence that current PM metrics were significantly stronger in explaining cover and richness in MFI species, despite the fact that proximities to mature forests did not change over time for the majority of silvicultural forest plots. However, if forests were at equilibrium with current landscapes then it would have been more logical to find that there were no differences in richness of MFI species among the four proximity change classes, since little change has occurred. In contrast, if MFI species richness was dependent on landscape configurations at the time of disturbance it would be logical to expect lower than expected richness levels within plots that have only recently become close to mature forest and higher than expected MFI richness levels for plots that have only more recently become isolated from mature forest. The results were contrary to these expectations. This suggests the auto-

correlation between the proximity change classes and other factors affecting species richness, such as disturbance history, has given rise to these perverse results. The three plots that declined in distance to mature forest had been old growth when logged and appeared to have been subject to cooler patchier regeneration burn than typical of most sites. This would explain the higher than expected richness levels of MFI species. In contrast all but one of the nine plots that had increased in distance had been regrowth forests when last logged (i.e. disturbed twice in previous century), which may have contributed to their lower than expected MFI richness levels. The confounding of these variables has obscured any capacity to determine to which PM temporal scale metric MFI species richness is actually responding. I conclude therefore that the results for the PM metrics provide insufficient evidence to reject the initial hypothesis (wet eucalypt forest floristic responses are most strongly influenced by landscapes at the time that the forest is disturbed). However, the lack of support from the PM metrics and the strong autocorrelation between LC metrics and site variables requires further consideration in the context of the results of other studies and observations.

5.5.2 Autocorrelations among metrics and site variables

The LCI metric is by design a surrogate for local disturbance history, so the strong correlation between the LCI metrics and disturbance frequency at the sites is no surprise, but rather an endorsement of the value of this metric as a tool for planning landscape management. It is also natural that landscape configuration, especially the historical landscape will be associated with rainfall patterns, drier areas being naturally more fire prone than wetter areas. Hence in any empirical study of a natural region it is almost inevitable that there will be a confounding of variables, making such natural experiments problematic.

It can be argued that the improved model performance for MFI species cover using the historical LCI metrics with other variables, provides sufficient evidence that these historical LCI metrics provide more explanatory power for this response than they would if they were only acting as simple surrogates for site variables. The weaker relationships with species richness is likely due to the complexity of successional dynamics in response to many factors, particularly disturbance history at the site and resulting legacies from earlier vegetation.

Because of the particularly strong autocorrelation among the PM metrics, it was not possible to rely on the comparative results to distinguish which LC metric was more important for the floristic responses. However because there was strong autocorrelation among the LCI metrics it was not possible to determine if the 500 m radius was better than 1 km radius for predicting floristic response to LC.

5.5.3 Efficacy of Landscape Context Index (LCI) versus proximity to mature forest (PM) metrics

The results demonstrated that LCI metrics did not have a uniformly stronger association with vascular plant floristic variation in wet eucalypt forest than log transformed PM metrics. MFI species cover, total species richness and relative richness of MFI species in silvicultural forests were all more strongly associated with the PM metric than with LCI metrics, although the differences were only marginal for MFI species cover and total species richness. Among the PM metrics the current year

distance to all mature forest communities (PM:MF:CY) provided a better explanation of the data than others.

In comparing the value of the two metrics for management planning, I conclude that the increased simplicity of working with distance metrics may outweigh the marginal benefits of improved model strength demonstrated in some cases with the more complex LCI metrics. The strong correlation between the LCI metric and PM metrics also suggests that either is likely to meet the needs of landscape management planning. Nevertheless, for species that respond to habitat abundance it is possible that the LCI metric will still provide a superior metric, as suggested by the lack of response by the avifauna to mature forest proximity whereas a clear response was evident in silvicultural regrowth when the LCI metric was used (Wardlaw et al. 2012; Hingston et al. 2014).

5.5.4 Conclusion

These results demonstrate that the LCI metric is associated with plant species assemblages but that it is the historical LCI metrics that explain current variation in assemblages, particularly within older regrowth and mature forest classes. The historical metrics were most strongly associated with mature forest species cover, while pioneer species richness was not associated with any of the metrics examined when site environmental variables were included in the models. Although there is support for the hypothesis that successional trajectories at a site are influenced by the landscape at the time they were last disturbed, it remains unclear to what extent the changes in surrounding landscape will continue to influence the successional trajectory of the community.

The results demonstrated that increased disturbance frequencies in the landscape that result in losses in mature forest abundance and reduced average proximity to mature forest habitat will result in slower recovery rates for mature forest species following disturbance.

"... For as far as two leagues the cedars shivered when Enkidu felled the watcher of the forest, he at whose voice Hermon and Lebanon used to tremble. Now the mountains were moved and all the hills, for the guardian of the forest was killed. They attacked the cedars, the seven splendours of Humbaba were extinguished. So they pressed on into the forest bearing the sword of eight talents. They uncovered the sacred dwellings of the Anunnaki and while Gilgamesh felled the first of the trees of the forest Enkidu cleared their roots as far as the banks of Euphrates. They set Humbaba before the gods, before Enlil; they kissed the ground and dropped the shroud and set the head before him. When he saw the head of Humbaba, Enlil raged at them, 'Why did you do this thing? From henceforth may the fire be on your faces, may it eat the bread that you eat, may it drink where you drink.' ... "

The epic of Gilgamesh, 2006 edition, translation by N.K. Sandars first published in 1960, Penguin Books, London, p. 23

Chapter 6 Landscape influence on forest establishment in old fields

6.1 Abstract

This chapter examines the floristic composition of wet eucalypt forest on sites that were cleared for agricultural production but later abandoned and naturally revegetated (old field sites). A comparison of species composition of the old field forests with wet eucalypt forest of the same age since last disturbance provided evidence that old-field forests have distinctive assemblages. Characteristics of old field regrowth forest included a higher species richness and a higher abundance and richness of forbs, graminoids, exotic plant species and species dispersed by vertebrates. Some plant group responses to mature forest influence within regrowth forests on old field sites also differed from the responses of these groups in regrowth at other sites. Richness of exotic species, richness of ground ferns and the cover of graminoids, cover of exotic species, all declined with increasing mature forest in the landscape in regrowth forest that had not been cleared. In contrast at old field sites there was either no evidence of a LC influence on these response variables or an opposite trend was observed in the response. Likewise although richness of epiphytic ferns increased in association with mature forest influence in most regrowth forest, there was no evidence that richness of epiphytic ferns at old field sites was influenced by LC. There was also evidence that LC metrics explained less of the similarity in composition between regrowth forest and mature forest, compared with the assemblage similarity between other regrowth forest and mature forest. The available evidence suggests that the successional trajectories of wet eucalypt forest on old field sites differ from other regrowth forest, and are less influenced by the abundance of mature forest in their surrounding landscape.

6.2 Introduction

The realisation that plant communities may change in predictable ways over time, and that the starting point may affect the trajectory of such change, led to the distinction between 'primary' and 'secondary' succession (Cowles 1899; Clements 1936). Egler

(1954) developed his successional theory of 'initial floristic composition' specifically to explain the observed patterns in the re-establishment of forest on abandoned farmland. A large number of studies of change over time in plant communities of old fields, from abandonment through to forest re-establishment, form the basis of current vegetation succession theory. The majority of this work focused on old fields of the temperate zone of eastern United States (Holl 2007). In the wake of native vegetation loss in many regions of the world, researchers are again returning to the study of succession in old fields, motivated increasingly by the desire to know if intervention might enhance native habitat restoration within highly fragmented landscapes (e.g. Standish et al. 2007, Elgar et al. 2014, Yeo and Fensham 2014). This research is becoming urgent, as the global rate of land abandonment has been increasing steadily since 1900, reaching more than 200 million hectares in the decade ending 1990 (Cramer et al. 2008). Regrowth vegetation has been establishing in one Central Victorian region at a rate of 1800 ha per decade since the 1960s and now comprises 12% of the region's land cover (Geddes et al. 2011).

A search in the Web of Science (May 2015) on the terms ('old field' and 'succession' and 'forest') for all available years returned 506 records since 1983, with an increasing trend over the last decade. Among the countries represented by the authors 54% (272) were from the USA and Canada, and only 3% (14) were Australian. Among the Australian studies only ten studied old field succession within the Australian region, of which only five investigated successional processes in plant communities (Ellis and Pennington 1992; Toh et al. 1999; Standish et al. 2007; Elgar et al. 2014; Yeo and Fensham 2014). Of these five, only Ellis and Pennington (1992) studied a temperate forest ecosystem, investigating the ways in which the germination and growth of the tree species *Eucalyptus delegatensis* was inhibited by the presence of native tussock grasses in cool montane regions of northeast Tasmania. At least one other published study of cool temperate forest old fields was not captured by the Web of Science search. That study, by Read and Hill (1983), demonstrated that bird dispersed shrubs were among the early invaders and were pivotal in creating nodes around which these and other species were then colonized. However, despite these nodes of reforestation, the dominant trees from the adjacent rainforest were mostly

restricted to the margins of the boundary, expanding incrementally into the old field area at a rate of only 5 m in three decades (Read and Hill 1983).

The pivotal role of birds in the recolonization of old fields has been observed in several other studies (e.g. Gasparri and Grau 2009). Neilan et al. (2006) found that subtropical old fields dominated by mature camphor laurel, a fleshy-fruited exotic tree, supported a rich diversity of native rainforest plants. Among the immature regrowth plants of these patches, 90 percent of species were native, 77% of which were capable of being dispersed by birds (Neilan et al. 2006). Toh et al. (1999) found that the presence of any trees, even those without fruit, but particularly trees larger than six metres in height, accelerated species recruitment. Likewise, a study of two small experimental sites in the tropics, found that the retention of live or dead trees or the placement of artificial bird perches, all led to increased colonization by both exotic and native species compared with open areas (Elgar et al. 2014).

Successional rates and trajectories may vary widely depending on the cultivation legacy, soils, and vegetation systems (Cramer et al. 2008). For example, Yeo and Fensham (2014) demonstrated that, despite landscape fragmentation, recruitment of late-stage species was occurring without active intervention by managers in *Acacia* dominated woodland regrowth established naturally on old fields in a tropical area. In contrast, Standish et al. (2007) report that there are significant barriers to recruitment of native species in the old fields of the heavily fragmented landscapes of the western Australian wheat-belt region. They conclude that the limits to dispersal of most species, and the competition from exotics, requires that direct seeding and control of exotic species is a pre-requisite for native habitat restoration for that region.

The aim of this chapter is to investigate the floristic composition of regrowth wet eucalypt forest located in old fields within a small region of Tasmania's Southern Forest and answer the following questions relevant to successional dynamics and landscape influence in these forests:

- Does regrowth composition on old fields differ from other regrowth?
- Is the floristic response to landscape context (LC) the same for regrowth in old fields as other sites?

- Is the similarity to mature forest and its response to LC the same for regrowth in old fields as other sites?

6.3 Methods

6.3.1 Study area

The study area comprised a region of about 7 x 7 km in size west of the township of Franklin (Figure 6.1). It is located within the far northeastern corner of the experimental forest landscape described in chapter 2. Within this agricultural hinterland, marginal land was cleared for farms in the late nineteenth and early twentieth century and later abandoned in response to economic depression and the wildfires of 1934. Much of this area was burnt again in 1967, so that regrowth on old-fields and adjacent uncleared forest areas are the same age. However, a large portion of the regrowth in this region was targeted for conversion to timber plantations in the last two decades leaving only small remnants, most of which are on private property and difficult to access.

6.3.2 Data collection

Four sources of data were used to determine the location of extant regrowth on old fields, and areas never cleared: the digital 1947 PI map and digital 2010 PI map (both described in chapter 2); the scanned and ortho-rectified copies of the original 1947 aerial photography, and satellite imagery in Google Earth viewed prior to sampling. Areas mapped as non-forest, agricultural land or plantations were erased from the areas that were mapped as agricultural land, bracken, or non-forest in 1947 to determine the possible extent of regrowth on old field sites. These potential study sites and the state cadastral data set were then overlaid on the 1947 aerial imagery to further refine potential sampling locations. Potential sites were next investigated with Google Earth to determine if they were native eucalypt forest. Permission to access the most spatially separated of these old field regrowth sites, as well as nearest regrowth and mature forest patches in uncleared forest, was then sought from land owners/managers.

Fifteen accessible patches of regrowth *E. obliqua/ E. regnans* wet forest growing on old fields at least half a hectare in extent were sampled (Figure 6–1). For each old-field regrowth patch, a comparable accessible patch of regrowth forest and an accessible patch of mature forest were also sampled from the surrounding area. Therefore, the final data set comprised 15 old field regrowth sites (P), 15 sites in uncleared regrowth (N) and 15 mature forest sites (M). The constraints of sampling resulted in some old field sites having the same nearest accessible regrowth or mature forest site as other old field site (Figure 6–1). All selected regrowth sites had dolerite substrates, which in this area are associated with chromosol soils, but varied in topographic position.

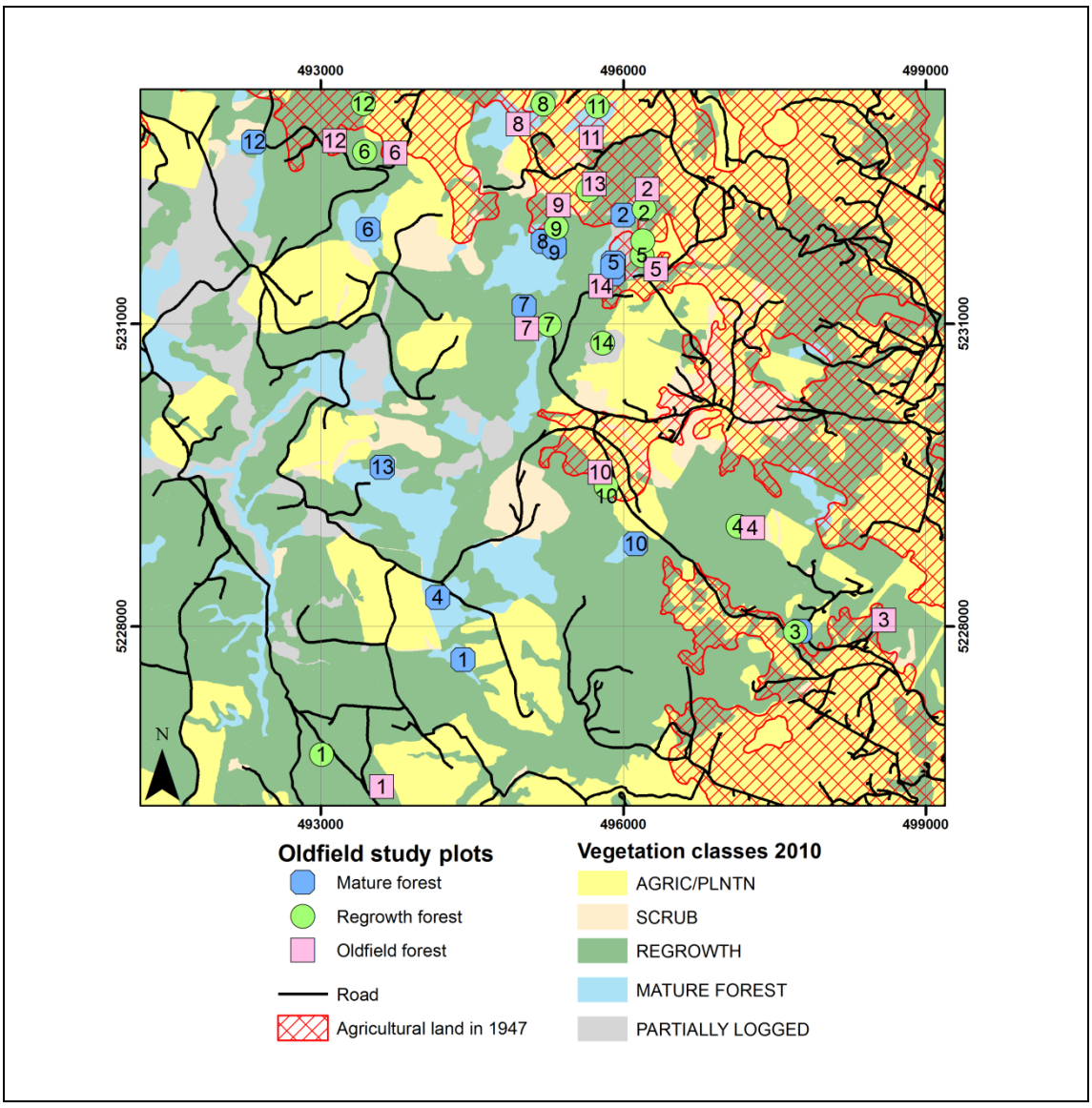


Figure 6-1. Distribution of plots by forest type.

The most accessible area of each site was sampled within a 50 by 50 m plot area using three 10 by 10 m quadrats, located randomly subject to the constraint that they were all at least 15 m from structurally different vegetation (e.g. pasture), more than 10 m from each other and did not share a common border. Within each 10 x 10 m quadrat the percentage projected foliage cover of all plant species present within the quadrat was estimated. For each plot the environmental parameters including easting and northing (MGA, to the nearest 20 m).

For each quadrat the Landscape Context Index score calculated for 1947 and 2009 landscapes using a buffer radius of 500 m was calculated. The LCI maps are described in chapter 2.

6.3.3 Statistical Analysis:

6.3.3.1 Does regrowth composition on old fields differ from other regrowth?

PERMANOVA was used to determine if the *a priori* treatment groups: 'old field' and 'uncleared' explained variation within a Bray-Curtis resemblance matrix of square root transformed, but otherwise unstandardized, cover data for regrowth forest quadrats. The model tested the fixed effect of treatment, nested within the random effects of site location (sites 1 to 15). Sums of squares were calculated using the TYPE III (partial) method recommended for balanced designs but compared with the full model and sequential models to check results were robust. A reduced model using 9999 permutations of residuals was adopted for testing all models. The PERMANOVA assumption of equal dispersion among the fixed factor groups were tested using permutational analysis of multivariate dispersions (Anderson et al. 2008).

Indicator species analysis (Dufrene and Legendre 1997) within the software package PCOrd 6.08 (McCune and Mefford 2011) was used to determine which species were indicators of old fields and which were most frequent and abundant in regrowth that had never been cleared. Only those species for which the difference in their distribution reached an alpha level of significance of 0.05 or less were accepted as indictor species of particular forest age-classes.

The total richness, and the richness and cover for five life form classes (epiphytic ferns; ground ferns including tree ferns; graminoids, including grasses; forbs; and woody plants) and for the Angiospermae five seed persistence/dispersal classes (soil stored; bradyspore; wind-dispersed; vertebrate-dispersed; poor dispersal and persistence) were tested to determine which differed in their response to treatment (old field versus uncleared forest). To test these responses, linear mixed effect (LME) modelling was undertaken by specifying the treatment as the only fixed effect factor with the region sampled (factor 1 to 15) specified as a random effect. The LME modelling was undertaken using Gamlss 4.3−0 (Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007; Stasinopoulos et al. 2014) within the R software platform (R Core Team 2014). The richness data were generally best modelled using the normal distribution family, but where the residuals suggested a poor fit, a Poisson distribution family was specified instead. The un-standardised percentage cover data (divided by 100) was tested first, using the zero inflated beta distribution. However, the residuals did not conform to normal. After adding one to the percent cover scores they were log transformed and reanalysed specifying a normal distribution.

6.3.4 Is the floristic response to LC the same for regrowth in old fields as other sites?

The software package, PCOrd 6.08 (McCune and Mefford 2011), was used to ordinate the data with non-metric multidimensional scaling (NMS), which has many advantages over other ordination techniques for displaying the similarities between sampled communities (Clarke 1993). A joint plot of the vectors for the 1947 and 2009 LCI metrics was superimposed on the ordination diagram to visualise the degree of association between each treatment and LC. The correlation between each ordination axis and each LCI index was also calculated.

LME was used again to test the association of the floristic responses with the fixed effect of LCI. The difference in the response between the treatments was tested by testing the significance of the interaction term between the factor treatment and LCI score.

6.3.5 Is the similarity to mature forest and its response to landscape context the same for regrowth in old fields as other sites?

Species covers, easting, northing and LCI scores, were each averaged for the three subplots in each 50 x 50 m plot for all three treatments (mature forest, old field and other regrowth sites) in each of 15 areas. This provided a data set of 45 plots. Distance matrices were generated for the assemblage data using Bray-Curtis dissimilarity index and for spatial distances using Euclidean distance in PCOrd 6.08.

For each regrowth plot the Bray-Curtis dissimilarities and distances to each of the 15 mature forest plots was extracted (n = 900). LME was then used to test whether the Bray-Curtis floristic dissimilarity to mature forest was the same for the fixed effects of treatments (old field versus other regrowth) given the random effect of the 15 sampled areas. The model was tested with and without the interactive or additive effect of geographic distance. The generalised linear modelling, also undertaken using Gamlss 4.3−0 within the R software platform, was used to test the results without taking account of the random effects of area. For this analysis, average dissimilarity and distance to mature forests of each regrowth plot was calculated (n = 15 per treatment). These models were used to test the effect of LCI on the association of the response variable.

6.4 Results

6.4.1 Does regrowth composition on old fields differ from other regrowth?

The 30 regrowth forest sites examined included a total of 97 understorey species and five species of eucalypt. Among the understorey species 63 were shared in common between the old field and uncleared sites, including only one exotic, *Rubus fruticosus*. The old field sites had 23 species not located in nearby uncleared regrowth. Seven of these were exotic species, six forbs and one woody plant. Of the 16 native species most were pioneer species typical of regrowth forest, including six graminoids, four forbs, three shrubs and one fern, all poorly represented in the data set. Only two were

considered to be rainforest species more typical of mature forest than young regrowth forest, both of which were ground ferns (*Asplenium flabellifolium* and *Sticherus tener*). The uncleared regrowth had 11 species not located in old field sites. None of these species were exotic, two were late-stage epiphytic ferns, and the rest were early-stage pioneer species (two forbs and seven woody plants).

Total species richness levels in the regrowth forest understoreys were higher in old fields than in areas not subject to conversion (Figure 6–2) mainly due to the higher number (and cover) of forbs at these sites (Figure 6–3). Slightly higher richness levels were also observed for exotic species and graminoids were observed for old field sites, but there was lower richness and cover of plants with a Tasmanian endemic distribution and epiphytic ferns (Table 6–1). Total cover of trees (including canopy eucalypts), did not differ between old field regrowth and uncleared regrowth (Figure 6–2) (old field coefficient -8.12 ± 4.61, t-value = -1.76, *P*-value = 0.082, untransformed cover data, normal distribution).

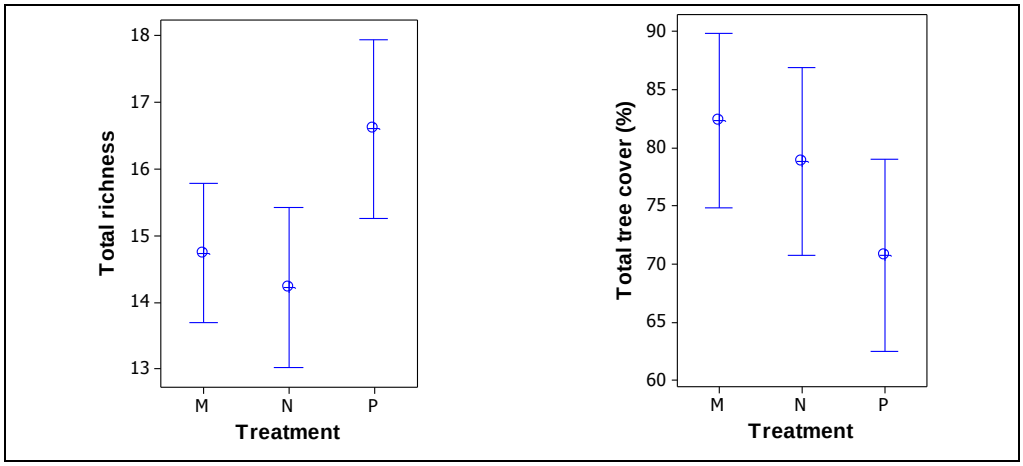


Figure 6-2. Mean and 95 % confidence intervals for total richness (left) and total tree cover (right) recorded for each forest treatment (M: mature forest; N: Never cleared, P: old field). Data shown includes eucalypt species.

There were much larger differences between treatments in the richness and covers of spermatophytes persistence and dispersal mechanism groups (Figure 6–4). The greatest effect was observed for plants typically dispersed by vertebrates, with much higher richness and cover levels recorded at the old field sites (Figure 6–4, Table 6–1). Smaller differences were also detectable in the richness and cover of species without specialised adaptations for dispersal or persistence ('nil'), for which there was

strong evidence for lower cover and weaker evidence for reduced richness levels at the old field sites (Table 6–1). The richness and covers of plants with soil stored seed banks were higher in old field sites, although the cover differences were only detected when the data were log transformed (Table 6–1). In contrast the covers of bradyspores were higher on old field sites but there was no difference in their richness levels (Table 6–1). No differences were found for wind-dispersed spermatophyte species (Table 6–1).

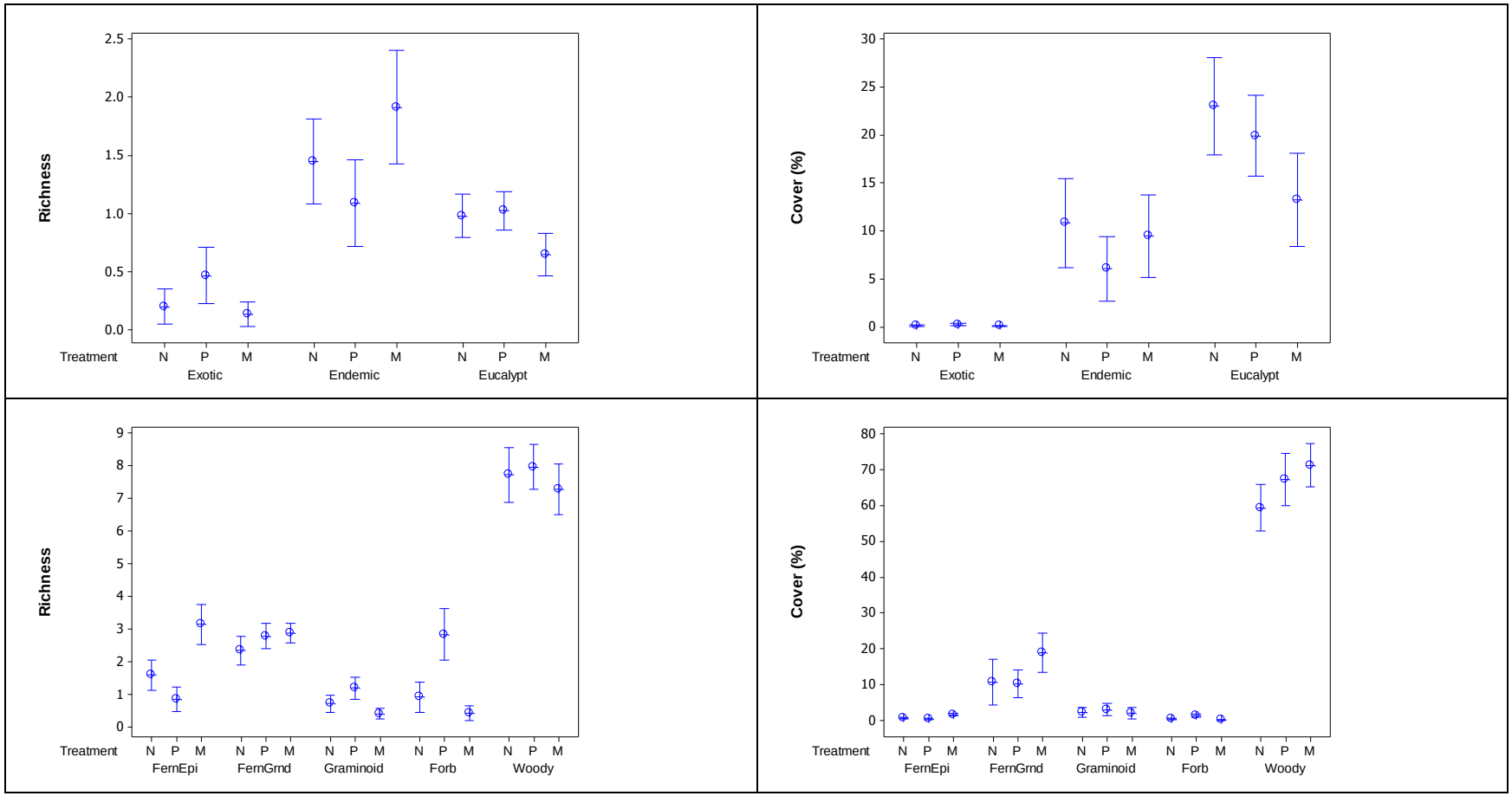


Figure 6-3. Mean and 95%confidence intervals for richness and cover by treatment portioned for life form and distributional groups.

Table 6-1. Richness and cover response to treatment (old field / not old field) of understorey plant species grouped by distributions, life forms and seed dispersal/persistence mechanisms [for notes see next page].

	Richness			Cover		
Groups	Old field mean (±std dev)	Not old field mean (±std dev)	Old field coefficient ±std error t-value (*P*- value)	Old field mean (±std dev)	Not old field mean (±std dev)	Old field coefficient ±std error t-value(*P*- value)
Total	15.6 (± 4.5)	13.2 (± 3.9)	2.33 ± 0.87 2.67 (0.009)			
Exotics	0.2 (± 0.4)	0.1 (± 0.3)	0.85 ± 0.37 2.30 (0.025 #)	0.2 (±0.4)	0.1 (±0.3)	n.s. 1.78 (0.078)
Endemics	1.1 (± 1.2)	1.4 (± 1.2)	-0.36±0.17 -2.14 (0.036)	6.1 (± 11.2	10.8 (± 15.5)	-0.66±0.22 -2.99 (0.004)*
Life Form Groups						
Epiphytic ferns	0.8 (± 1.2)	1.6 (± 1.2)	-0.73± 0.25 -2.91 (0.004)	0.4 (± 0.6)	0.8 (±0.8)	-0.22±0.07 -2.98 (0.004)*
Ground ferns (incl. tree fern)	2.8 (± 1.3)	2.3 (± 1.5)	n.s. 1.69 (0.09)	10.3 (± 13.2)	10.7 (±21.2)	n.s. 1.61 (0.11)
Graminoids	1.2 (± 1.1)	0.7 (± 0.9)	0.46 ± 0.17 2.77 (0.007)	3.1 (± 5.6)	2.3 (±4.8)	n.s. 1.31 (0.19)
Forbs	2.8 (± 2.6)	0.9 (± 1.6)	1.91 ± 0.40 4.77 (0.000)	1.4 (± 1.3)	0.5 (± 0.8)	0.46 ±0.09 5.24 (0.000)
Woody plants	8.0 (± 2.3)	7.8 (± 2.8)	n.s. 0.55 (0.58)	67.3 (± 24.3)	59.3 (± 21.6)	n.s. 1.98 (0.052)
Spermatophyte dispersal/persistence groups						
Nil	0.3 (± 0.5)	0.4 (±0.7)	-0.35 ± 0.17 -2.02 (0.05 #)	2.0 (± 8.6)	19.6 (± 19.3)	-0.53 ± 0.15 -3.45 (0.0009)
Soil seed bank	4.5 (± 2.1)	2.7 (± 2.3)	0.50 ± 0.13 3.90 (0.0002#)	28.7 (± 23.3)	23.4 (± 24.3)	0.59 ± 0.19 3.11 (0.0027)*
Bradyspore	1.3 (± 0.8)	1.2 (± 0.8)	n.s. 1.45 (0.14 #)	4.7 (± 11.5)	0.9 (± 3.1)	0.39 ± 0.17 2.33 (0.022)
Wind	2.4 (± 1.3)	2.3 ± 1.1	n.s. 0.18 (0.85)	18.0 (± 22.3)	21.6 (± 21.2)	n.s. -1.55 (0.13)
Vertebrate	4.6 (± 2.1)	3.8 ± 1.8	0.82 ±0.34 2.42 (0.018)	18.3 (± 16.6)	6.7 (± 7.6)	0.93 ± 0.16 5.97 (0.0000)

Table 6–1. Analysis notes:

Eucalypt species are excluded from the data analysed;

^ Results for tests using linear mixed effect modelling specifying a normal family distribution unless otherwise indicated, note that cover data were log transformed prior to analysis; # Poisson distribution; $^{+}$ Negative binomial distribution; * indicates results transformed cover data were contrary to results for untransformed data using a beta distribution (data not shown). n.s.: Not significant.

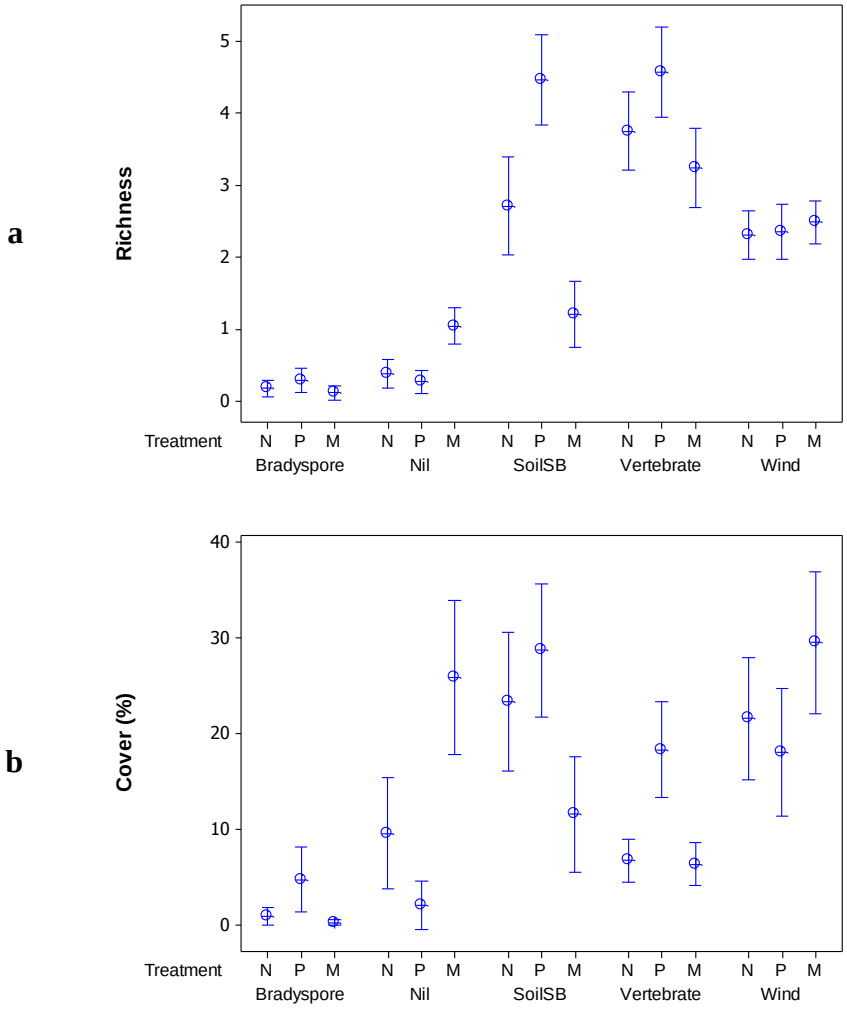


Figure 6-4. Mean richness (a) percentage cover (b) showing 95% confidence interval for all understorey species of spermatophyte (including exotics, but excluding eucalypts) grouped by treatment and persistence/dispersal class.
(Treatment: N = Regrowth never cleared, P = Regrowth on old field, M = Mature forest)

Table 6-2. Summary table of PERMANOVA results for assemblage variation by treatment

Source	Degrees freedom	Sums Squares	Mean squares	Pseudo-F	*P*(perm)	perms	Sq.root ECV
Site	14	113600	8114	8.87	0.0001	9793	34.6
Treatment (nested in Site)	15	74412	4961	5.42	0.0001	9817	36.7
Residual	60	54870	915				30.2
Total	89	242880					

The results of a PERMANOVA analysis also demonstrated that there was an overall difference in the assemblages of regrowth depending on whether the regrowth was on an old field or not (Table 6–2). Similar results were obtained regardless of whether the data were standardised and/or square root transformed, or whether the hierarchical structure in the data set was accounted for in the PERMANOVA design or not (data not shown). There was no evidence from the results of the PERMDISP analysis that the multivariate dispersion among the two treatment classes were different (F = 1.41, df1 = 1; df2 = 88, *P* (perm) = 0.28).

The NMS ordination chart illustrates the separation between regrowth types although there was also an overlap in their floristic composition (Figure 6-5). The alignment of the vectors for the richness and cover of life form and dispersal/persistence groups supports the results of the statistical analyses, demonstrating that weeds, forbs and spermatophytes distributed by vertebrates are the most strongly associated groups with regrowth on old field sites, while the epiphytic ferns were most strongly associated with regrowth that had never been converted (Figure 6–5).

The results of the indicator species analysis provided evidence that there were more species distinguishing the regrowth in old fields compared with unconverted areas (Table 6–3). Among these were the fleshy fruited species such as *Coprosma quadrifida*, *Gaultheria hispida*, *Pittosporum bicolor* and *Tasmannia lanceolata* (Table 6–2). The wind-dispersed pioneer species *Cassinia aculeata* was also identified as an indicator of old field regrowth. Only one weed, *Centaurium erythraea*, was sufficiently frequent in old field regrowth to be identified as an indicator of this regrowth type (Table 6–3).

Table 6-3. Indicator species of old field and other regrowth communities

	Life	Succession	Distribution	Dispersal	Untransformed cover data		Square Root Transformed	
Species name	form	Stage		persistence	Indicator Value	*P* (perm)	Indicator Value	*P* (perm)
Uncleared regrowth	class	class		class				
Atherosperma moschatum	Tree	Mature		Wind	27.1	0.0420	28.6	0.0119
Bedfordia salicina	Tree	Pioneer		Wind	27.9	0.0662	29.5	0.0230
Grammitis billardierei	Epiphytic fern	Mature			35.6	0.0326	35.6	0.0345
Nematolepis squamea	Tree	Pioneer		Soil seed bank	21.7	0.0214	19.5	0.0321
Old field regrowth								
Acacia dealbata	Tree	Pioneer		Soil/Wind	40	0.0041	37.1	0.0067
Acaena novae-zelandiae	Forb	Pioneer		Vertebrate	30.6	0.0021	30.6	0.0029
Cassinia aculeata	Tree	Pioneer		Wind	40.8	0.0006	37.2	0.0007
Centaurium erythraea	Forb	Pioneer*	exotic	Wind	15.8	0.0267	15.8	0.0305
Coprosma quadrifida	Shrub	Pioneer		Vertebrate	75.9	0.0001	63.6	0.0001
Gaultheria hispida	Shrub	Mature		Vertebrate/Wind	16.2	0.0250	16	0.0240
Geranium potentilloides	Forb	Pioneer		Soil seed bank	36.5	0.0001	36.5	0.0005
Hydrocotyle hirta	Forb	Pioneer		Soil seed bank	43.8	0.0001	43.6	0.0001
Leptospermum lanigerum	Tree	Pioneer		Bradyspore	20.8	0.0239	19.6	0.0257
Pittosporum bicolor	Tree	Mature		Vertebrate	44.5	0.0665	43.3	0.0430
Polystichum proliferum	Ground fern	Mature			41.8	0.0499	36.4	0.0620
Pteridium esculentum	Ground fern	Pioneer			65.6	0.0002	56.2	0.0002
Senecio spp.	Forb	Pioneer		Wind	29.7	0.0184	29.7	0.0191
Tasmannia lanceolata	Shrub	Mature		Vertebrate	48.9	0.0291	28.6	0.0119

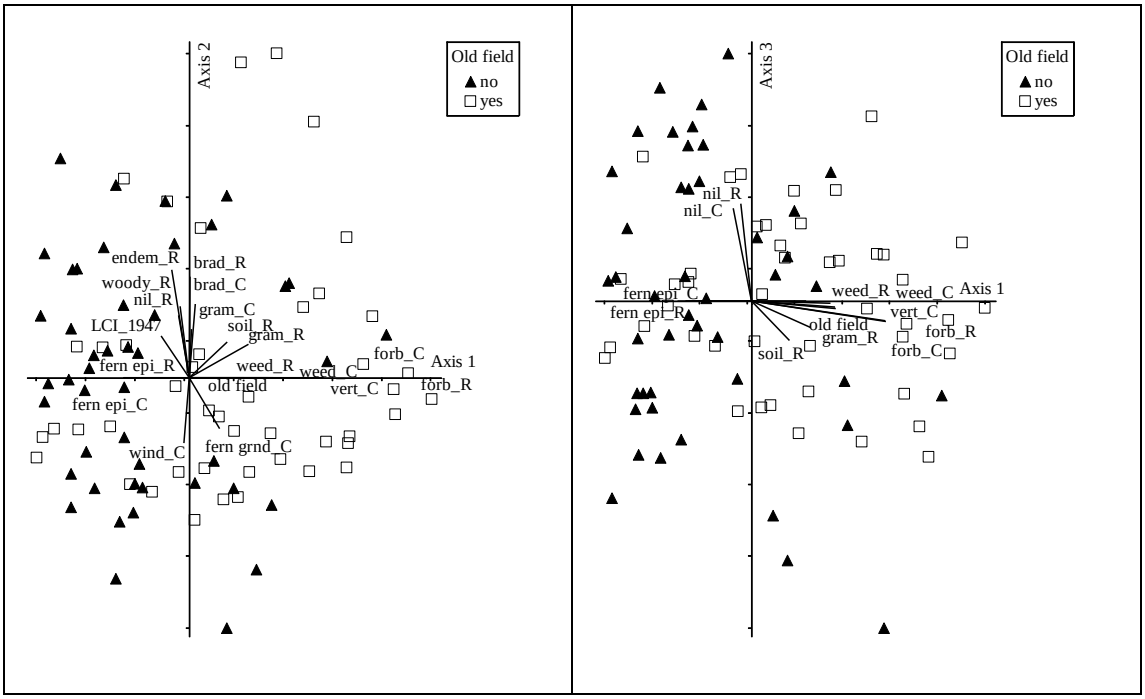


Figure 6-5. NMS ordination (square root transformed cover data) overlaid with vectors for richness and cover scores for plant species groups and LCI scores correlated with species assemblage variation (100% scale, cut off R^2 = 17%). Ordination rotated to align with old field plot distribution. The first two axes explained 28%, and 32% respectively of the variation, while the third axis explained only 18%. The stress of the final solution was 16.3.

6.4.2 Is the floristic response to landscape context the same for regrowth in old fields as other sites?

Overall there was evidence that the composition of the regrowth forests was associated with LCI, most strongly with the 1947 landscape LCI scores (LCI 1947 correlation with NMS axis 2: Pearson R = -0.53, R^2 = -0.27, Figure 6-5). Likewise, the results of linear mixed effect modelling also provide evidence of an overall association between LCI scores and several floristic responses within regrowth forests generally, including increasing richness of endemic species, an increasing cover and richness of species without specialised adaptations for dispersal and persistence, and a decreasing cover and number of forbs (Table 6–4).

The fitted vectors for LCI scores superimposed on the ordinations for old field regrowth and other regrowth illustrates that the difference in floristic response to these

metrics was not strongly evident in the ordination (Appendix 6.5.1). Nevertheless, results of LME modelling, which included an interaction term for treatment and LCI, provided some weak evidence that several floristic responses varied depending on whether the regrowth was on old fields or not (Table 6–4). However, the lack of adequate replicate samples across the range of LCI scores means that outliers may have unduly affected some results.

Richness of exotic species, richness of ground ferns and cover of graminoids declined in association with LCI for regrowth forest not subject to a history of conversion, but either there was no evidence for an association between these responses and LCI or in the case of graminoid cover, the evidence suggested an increase with LCI on old field sites (Table 6–4, Appendix 6.5.2, Appendix 6.5.3). Richness of epiphytic ferns or species without adaptation for dispersal or persistence were not associated with LCI in regrowth on old fields but at other regrowth sites the richness of these two species groups increased with LCI (Table 6–4, Appendix 6.5.2). In the case of endemic species richness and covers, the positive association with LCI appeared to be only marginally stronger for old field sites than other sites (Table 6–4, Appendix 6.5.3: Figure 6–8). Likewise, the slight increase in bradyspore species richness and cover associated with LCI was only marginally stronger than that observed for other treatments, which was insufficient to provide evidence for an overall positive association with LCI (Table 6–4, Appendix 6.5.2, Appendix 6.5.3). There was no evidence for any interaction between wind dispersed species richness or cover, and the minor evidence for a decline in the cover of vertebrate dispersed plants was due only to the influence of a few outliers (Table 6–4, Appendix 6.5.2, Appendix 6.5.3).

Table 6-4. Life form group cover and richness associations with LCI and interaction between LCI and treatment (old field versus not old field). For explanation of codes see notes below table.

	Richness		Cover	
Groups	LCI Old field co-efficient t-value (*P, $*)^	Interaction Old field co-efficient t-value (*P, $*)^	LCI Old field co-efficient t-value (*P*-value,$)^	Interaction Old field co-efficient t-value (*P*-value, *$*)^
Total	1.62 (0.11, C)	1.23 (0.22, C)		
Exotics	n.s. -1.70 (0.09,H#)	0.98 ± 0.43 2.31 (0.024, H, #)	n.s. -1.64 (0.10, H)	n.s. 0.93 (0.35, H)
Endemics	0.48 ± 0.11 4.14 (0.0004, H)	0.33 ± 0.14 2.36 (0.021, H)	0.48 ±0.12 3.97 (0.0002 H)*	0.38 ± 0.19 2.01 (0.048 H)
Life form classes				
Epiphytic ferns	n.s. 1.13 (0.26, C)	-0.44 ± 0.21 -2.11 (0.038, H)	n.s. 1.12 (0.27, C)	n.s. -1.95 (0.055, H)
Ground ferns (including tree-fern)	n.s. 1.26 (0.21, H)	0.60 ± 0.25 2.39 (0.0197, H)	n.s. -0.27 (0.78, C)	n.s. 0.39 ± 0.19 2.03 (0.046, C)
Graminoids	n.s. -0.75 (0.45, C)	n.s. 1.68 (0.09, C)	n.s. -1.18 (0.24, C)	0.31 ± 0.14 2.28 (0.026, H)
Forbs	-0.59 ± 0.21 -2.68 (0.009, H)	n.s. 0.37 (0.71, H)	-1.16 ± 0.061 -3.54 (0.007, H)*	n.s. 0.38 (0.71, H)
Woody species	n.s. -0.23 (0.82,C)	n.s. 1.39 (0.17 H)	0.12 ± 0.05 2.34 (0.022, H)	n.s. -1.42 (0.16, C)
Spermatophyte dispersal/persistence class				
Soil seed bank	0.33 ± 0.12 2.82 (0.006,H#)	n.s. -1.57 (0.12,H#)	-0.52 ± 0.15 -3.45 (0.0009, H)*	0.53 ± 0.15 3.63 (0.0005,H)*
Bradyspore	n.s. 0.76 (0.45,H#)	0.83 ± 0.38 2.19 (0.03, H#)	n.s. 1.21 (0.23, H)*	0.31 ± 0.14. 2.22 (0.030, H)*
Wind	n.s. -1.18 (0.24, H)	n.s. -0.94 (0.35, H)	n.s. -0.68 (0.50, H)	n.s. -0.80 (0.42, H)
Vertebrate	n.s. -1.38 (0.17 H)	n.s. 0.47 (0.64,H)	n.s. -1.43 (0.16, H)	-0.36 ± 0.15 -2.39 (0.020, C)*
Nil	0.37 ± 0.16 2.40 (0.019, C#)	-0.34 ± 0.15 -2.24 (0.028, C#)	0.57 ± 0.11 4.80 (0.0000, H)	n.s. -1.19 (0.24, H)*

Table 6–1: Analysis notes

^ Results for tests using linear mixed effect modelling specifying a normal family distribution unless otherwise indicated, note that cover data were log transformed prior to analysis; # Poisson distribution; $^{+}$ Negative binomial distribution; * indicates results transformed cover data were contrary to results for untransformed data using a beta distribution (data not shown). n.s.: Not significant.

$: Results are reported for the LCI score with the strongest association to the response. The metric for which the data is presented is specified after the *P*-Value: Historic H, LCI 1947; Current C, LCI 2009.

6.4.3 Is the similarity to mature forest and its response to landscape context the same for regrowth in old fields as other forest?

The ordination diagram for all 45 plots (Appendix 6.5.4) demonstrated that the assemblages of mature forest communities were relatively distinct from the assemblages of regrowth forests, but there was little visual evidence to suggest regrowth forests of old fields were more or less similar to the mature forest assemblages than regrowth on other sites. Nevertheless, there were some regrowth plots that had achieved a community assemblage with more similarities to the mature forest than other regrowth. Old field sites and sites that had never been cleared were both represented among these successionally advanced communities (Appendix 6.5.4).

LME modelling provided evidence that the fixed effect of treatment was associated with regrowth similarity to mature forests, and that regrowth on old fields had a greater dissimilarity to mature forest than regrowth of other sites. The model was further improved by including the fixed effect of the interaction between log distance and treatment, and to a much lesser extent, by the addition of LCI score for each regrowth plot in 1947 (Table 6–5). The interaction term provided evidence that while other regrowth sites became less like mature forests the further away from them they were, no such trend was evident among the regrowth on old fields (Table 6–5, Figure 6–6). Comparative analyses all provided the same results (e.g. using untransformed cover data, a normal distribution, excluding the random effects of area sampled and specifying the mature forest plot as the random effect). The lowest BIC score was obtained when the random effect of the mature forest plots were specified but the distribution of the residuals was poorer (data not shown).

Table 6-5. Result summary of linear mixed effect model for mean Bray-Curtis dissimilarity to mature forest ^

Final model terms	Coefficient	Std.Error	t-value	*P*-value
(Intercept)	-0.9205	0.3982	-2.31	0.0213
Treatment (old field)	2.8468	0.5235	5.44	0.0000
Log distance	0.1523	0.0457	3.33	0.0009
LCI 1947	-0.1351	0.0494	-2.73	0.0065
Treatment (old field) X log distance	-0.3421	0.0677	-5.06	0.0000

^ Notes about LME analysis:
Dissimilarities between each regrowth plot and each of the 15 mature forest using square root of average cover (n = 450, degrees of freedom = 431)
Random effects of 15 areas sampled; beta distribution family.
See Figure 6–15 for residual diagnostic plot.

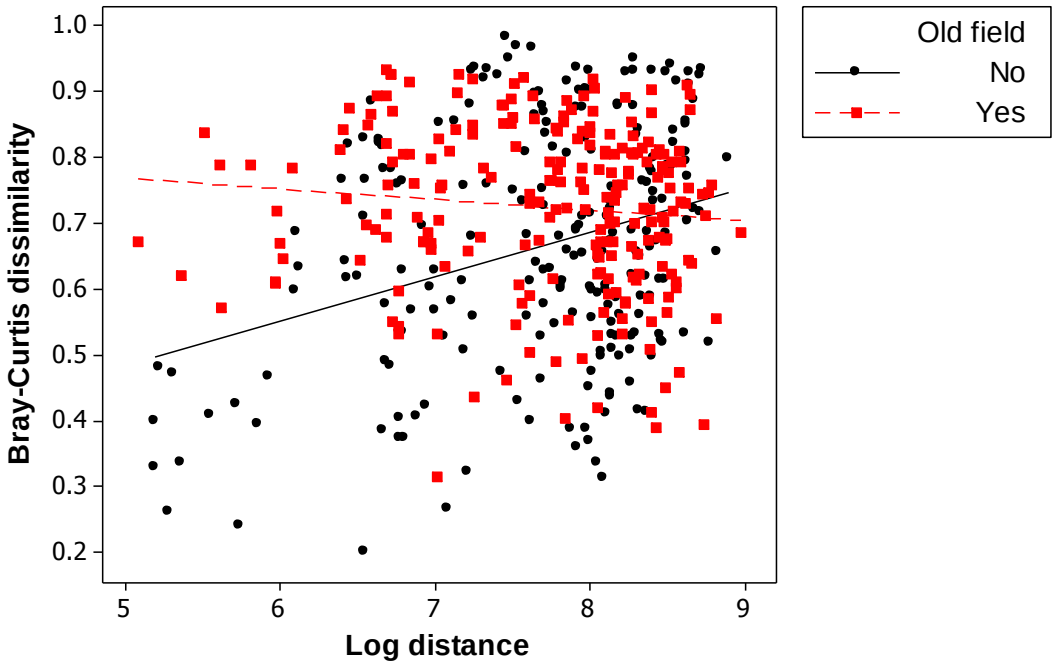


Figure 6-6. Scatter plot of regrowth dissimilarity to mature forest scores showing their relationship to log distance between plots and treatment (old field or not).

6.5 Discussion

6.5.1 Regrowth composition

The old field forests were largely devoid of tree growth in 1947 but were all mapped as young forests by 1984. In most of these old fields, logs were visible in the 1947 imagery, uncleared relicts from the earlier forest, a feature also observed for the old fields of northern Tasmania by Read and Hill (1983). Given that these old fields were on the frontier between intact native forest and more intensely developed agricultural areas, it seems probable most had not been subject to fertilizing, although they were in areas with naturally fertile soils. Their distance from other agricultural land, would also have made fertilizer drift unlikely. In these circumstances native forest was able to re-establish within four decades of abandonment, without the need for management intervention. By 2011, up to six decades since abandonment, the surveyed forests had only a negligible cover of exotic species and it appeared likely that most of the remaining weed species, with the possible exception of blackberry, may be eliminated, given sufficient time without further disturbance. The exact disturbance history since abandonment is not known but most areas sampled showed evidence of fires more recent than 1947.

A more detailed, but still unpublished, study of four old fields on dolerite substrates in southern Tasmania by Appleby (1998) provides a useful reference to compare with the results of the present study. His surveys were undertaken after only one to two decades of abandonment following more than six decades of grazing. After this shorter period of abandonment both improved pastures in high rainfall sites and the two unimproved pastures of drier sites had advanced very little towards achieving a forest cover, and the cover that had developed was mainly confined to the edge within 20 m of forest, with almost none extending beyond 40 m. The contrasting observations from the results of the present study suggest either there is a slower recovery in pastures that have been improved or in native pastures where conditions are drier, or else the expansion of cover by native trees and shrubs is non-linear, becoming increasingly rapid in the third or fourth decade after abandonment. A chronosequence of old fields in tropical northeastern Puerto Rico provided evidence that recovery rates do increase with time since abandonment, and had also achieved a

typical forest structure within 40 years (Aide and Zimmerman 1996). Matlack (1994b) noted that it took 30 years in Pennsylvania for secondary forest to achieve full canopy closure after fields had been abandoned. Further evidence for the non-linear invasion by plant species is available within studies of the naturalization of alien plants. Among this literature it has been reported that plant species dependent on mutualist-organisms such as mycorrhizal fungi have a lower rate of naturalization than that of plant species not requiring such associations (Dickie et al. 2010; Pringle and Vellinga 2006). A comparative study Dickie et al. (2010) of one naturalized and one endemic tree in New Zealand demonstrated that these two co-occurring species shared few native ectomycorrhiza, all of which had a cosmopolitan distribution. The native tree was associated with a rich native fungal community among which no non-native fungi were recorded. In contrast, the alien tree was associated with a depauperate community of mainly introduced ectomycorrhiza (Dickie et al. 2010). Their results provide evidence that the naturalization of *Pinus contorta* was dependent on the co-invasion of introduced ectomycorrhiza. It is probable that re-colonization of many native species is like-wise dependent on the facilitative presence of mutualist-organisms before they can establish successfully after disturbance. The rates of arrival of species is unlikely to proceed in a linear fashion.

The data set examined here was small, necessitating caution in the interpretation of results. Furthermore, the variation in regrowth assemblages was large for both old field and non-old field areas, lowering the confidence that observed differences were caused only by treatment differences. However, given that few native species were observed from this region that were not located within the old fields, it would seem unlikely that there would be any species that could not ultimately re-establish in the old field areas given propagule sources and time. Indeed, even after only ten to twenty years, Appleby (1998) found that there were only a few native species of the adjoining forest areas that had not successfully colonized the old fields despite low woody native vegetation cover.

While the regrowth forests on old fields shared a great deal in common with regrowth of similar age in uncleared neighbouring areas, the present study demonstrated differences between their assemblages. However, the variation between old field and other regrowth was less than the variation observed between areas (Table 6–2).

The greater importance of vertebrate-dispersed species in old field areas than in regenerated forest has been observed elsewhere (Read and Hill 1983; Toh et al. 1999; Neilan et al. 2006). Appleby also notes that vertebrate-dispersed plants occur at greater distances from the forest edge than plants with other dispersal mechanisms, but in his communities most were native forbs and graminoids dispersed by mammals. Fleshy fruited woody species dispersed by birds, such as *Tasmannia lanceolata*, *Coprosma quadrifida* and *Pittosporum bicolor* were all absent from the adjacent forest communities of the old fields of his study. Interestingly, the fleshy-fruited bird dispersed plants, *Cassytha pubescens,* and *Leptomeria drupacea*, although present in the native forest communities of his study were absent from the adjacent old fields. Both of these species are hemi-parasitic, a characteristic that may explain the apparent delay in their colonization, although at the drier old field another bird-dispersed hemi-parasite, *Exocarpos cupressiformis,* had colonized into the old field.

While greater dispersal capacity of seed may partially explain the success of vertebrate-dispersed plants, other ecological attributes are needed to explain why these species are not equally successful in establishing after wildfires or timber harvesting. Read and Hill (1983) observed that the greater success of bird-dispersed shrubs may be due to the higher probability that seeds are deposited in locations suited for establishment (i.e. below the shelter of an existing tree, or on logs, out of reach of browsers and free of competition from grasses). The greater energy resource invested in larger seeds or which is associated with seed deposits in bird regurgitate or animal scats is likely to enhance germination, early growth and increase capacity to withstand competition by pasture grasses (Tilman 1990). The trade-off for investing more energy in larger seeds is that these species usually produce fewer seeds than smaller seeded plants (Tilman 1990). The reduced rate of seed arrival compared with more fecund species, is likely to disadvantage vertebrate dispersed species after fire or timber harvesting where there is a relatively short time available before canopy closure. Therefore, the initial barrier to germination provided by pasture grasses in old fields may well confer an advantage to some vertebrate-dispersed species compared with smaller seeded plants. The rapid germination and competition from faster growing species is likely to reduce the performance of vertebrate dispersed species in forest areas disturbed by wildfire or timber harvesting.

No differences in richness or cover of wind-dispersed species was detected between regrowth on old fields and other sites, which also suggests that dispersal alone is not important in determining the success of colonists in old fields. Among the wind dispersed species there are some that were more successful at colonizing old fields, especially *Cassinia aculeata*, a species well known as an early pioneer of wet forests (Serong and Lill 2008). It is often the dominant early colonizer in many old fields in Tasmania and Victoria (Read and Hill 1983; Appleby 1998; Geddes et al. 2011). In contrast to this early pioneer tree, Read and Hill (1983) observed that colonization by the wind-dispersed rainforest tree, *Atherosperma moschatum*, was restricted to the same incremental rate of expansion from the rainforest edge as the poorly-dispersed rainforest tree *Nothofagus cunninghamii*.

The difference detected in the distributions of epiphytic ferns is likely to be because of the lack of structural elements upon which these species are dependent (mature trees, logs). Although not compelling statistically, the data did demonstrate that the old field regrowth had a slightly more open canopy/ sub-canopy structure and it is likely that there were also some unrecorded structural differences due to compositional differences (e.g. more open and senescing canopies of *Cassinia aculeata*). These differences may have resulted in greater light to the ground in the old field forests, potentially contributing to a microclimate less conducive for the establishment of epiphytic ferns. More light in the understorey of old field forests or perhaps a lag in the response by the light dependent plants to any more recent reductions in light, might also explain the higher richness and cover of forbs and the higher richness of graminoids in the old field forest compared with other sites.

The trend of higher richness and cover of herbs in these old field forests is counter to trends observed in the temperate forests of Europe and northern America, in which old field forest communities lack forest herbs (Flinn and Vellend 2005; Matlack 1994a). However, within the old growth forests and rainforests of Tasmania, herbs usually form a relatively minor part of the community. Most occur only after soil disturbance in tree fall gaps and are typically early pioneer species, more common in secondary forests after catastrophic disturbance (Gilbert 1959; Jackson 1968; Jarman et al. 1984). The *Eucalyptus regnans* forests in Victoria differ somewhat from those in Tasmania by their greater importance of herbs, a characteristic which presumably

reflects a more open canopy structure in the forests of lower latitudes (Kirkpatrick et al. 1988, unpublished data).

The reduced richness and cover of species lacking in adaptations for dispersal or persistence require no explanation, and are consistent with findings by Read and Hill (1983). Among the species classed as having a soil seed bank were a large number of exotic and pioneer herbs, which is sufficient to explain their higher richness in old field regrowth forest. The increased cover of bradyspore plants and plants with soil stored seed bank was perhaps more of a surprise, but is consistent with the results of Ellis (1985) and Appleby (1998). The former group, while represented by few species, among which was *Leptospermum lanigerum*, produce massive amounts of very fine seed, which is likely to disperse over distances of up to 50 m. The sheer number of seeds, particularly following fire events when mineral soils are exposed, would explain their success in colonizing old fields, at least following fire, although perhaps not their higher cover. *Acacia dealbata* was the species that contributed most to the high covers of species with soil seed banks. This species is well known as a successful early pioneer and colonizer of old fields in southeastern Australia (Gilbert 1959; Ellis 1985). In addition to having long-lived soil-stored seed, the seed pods are able to be carried relatively long distances in strong wind, enabling their distribution over more than 100 m (personal observation). They are also eaten by parrots (personal observation) and marsupials (David Lindenmayer personal communication, October 2015) and may be transported over further distances by these animal vectors. The greater cover of both these fast growing pioneer species in old field regrowth is likely to be a response to the absence of mature eucalypt trees and reduced density of regrowth eucalypt trees forming the canopy.

6.5.2 Effect of landscape context

The highly varied forest composition, small sample size, and the lack of good replication across the range of LCI scores, renders only a low confidence in the results observed in relation to the landscape effects on composition of regrowth forest in old fields compared with other sites. Nevertheless, many of the observed trends were consistent with expectations.

An increase in endemic species with increased LCI is likely to be consistent with Tasmania wide-trends showing a higher representation of plant species endemic to Tasmania among the primitive rainforest flora compared with the more recently evolved Australian element in wet forest (Jarman and Brown 1983; Kirkpatrick and Brown 1984a, b). However, there is no particular reason why either the cover or richness of these species might show a stronger gradient of increase in association with increasing LCI scores in old field sites than in other uncleared areas.

The trend of no association with LCI in old fields for exotic species richness and ground fern richness and cover, while the richness of these two plant groups decreased with LCI in other regrowth areas seems quite plausible, and is consistent with the forest in old fields being more open now and perhaps more so in the recent past compared with other regrowth across the range of LCI sampled. Although the interaction term between regrowth type and LCI score did not reach an alpha level of significance for forbs, the decline observed for forb richness in old fields was less pronounced that that associated with increasing LCI for other regrowth areas.

The lower levels, within old fields, of epiphytic ferns and species without adaptations for dispersal or persistence explained the lack or weaker response by these species to LCI compared with the stronger increase in richness of these species associated with increased LCI in other regrowth forests.

Both forest types showed the same increasing response to LCI for all woody plants, and richness of plants with soil stored seeds — a trend which might reflect a preference by these species for intermediate intervals of disturbance rather than the high levels of disturbance associated with the low levels of LCI in this small, relatively disturbance prone region (Grime 1973).

The absence in association with LCI for either the wind or vertebrate dispersed plant richness is consistent with these species being well dispersed and limits to their dispersal not having been reached within the study area for either treatment group. The association between increasing covers of vertebrate dispersed plant groups and LCI score which was only apparent within the regrowth forests that had not been cleared, seems likely to be the effect of outliers in the data set rather than founded in

any real difference between these two treatments with respect to LCI; if anything, a reduced cover in the abundance of these species with reducing disturbance levels would have been more likely to have occurred given their reduced capacity for competition from other woody plant species.

6.5.3 Successional trajectory to mature forest

The results from this small data set demonstrate that regrowth in old fields was less like mature forests communities than other regrowth forest of matching age in the area. The species contributing most to the greater difference in floristic composition with mature forest in regrowth on old fields included the dominant rainforest trees, which included poorly dispersed species such as *Nothofagus cunninghamii* and *Eucryphia lucida*, as well as *Atherosperma moschatum*. The lack of epiphytic ferns and the presence of weeds would also have contributed to the greater observed dissimilarities to mature forest in regrowth of old fields.

Like Aide and Zimmerman (1996), this study has found that there was no apparent landscape effect in the overall similarity of these old field areas and mature forest, a result which differs from other studies of landscape effects in old fields (e.g. Matlack 1994a; Neilan et al. 2006). Yet a landscape effect was observed in association with the variation in similarity to mature forest of other regrowth forests in the same region. The reasons for the difference are likely again to be the general lack of recruitment in both rainforest trees and epiphytic ferns and must reflect a barrier to recruitment imposed by more than just dispersal distances, a result observed by Standish et al. (2007) for vegetation in the old fields of Western Australia. However, most rainforest species were observed within at least some of the old field sites, and it seems likely that they will recruit more slowly into these sites given enough time free of disturbance. It is likely, therefore that over time, a LCI effect will begin to become apparent.

This study did not examine relationships between regrowth age and changes in similarity to mature forest in either old field or other sites. Other studies (e.g. Matlack 1994a; Yeo and Fensham 2014) have demonstrated that successional processes do occur in old field regrowth forests. These processes ensure that the composition of old

field forests become more similar to mature forest with time, a pattern that is likely to occur within the forests of this study. Despite this likely pathway, Leeson and Kirkpatrick (manuscript in submission) reported that floristic similarity between old field vegetation and vegetation on uncleared sites paired for their shared environmental characteristics were more dissimilar when old field vegetation had been abandoned for a greater length of time. Their results, suggest the possibility of alternative successional trajectories, which may well occur if some species fail to recruit, and others which are usually lost during the successional process are maintained.

6.5.4 Conclusion

Old field forest communities were more dissimilar to mature forests and appeared relatively unresponsive to changes in landscape context compared with other regrowth forest. Differences in the floristic composition within old fields from that of other neighbouring regrowth forest reflect differences in the barriers to colonization posed by pasture compared with the environment following fire in other secondary forest regrowth. Native species that are advantaged by conditions available in old fields include those with large seeds, especially those dispersed by vertebrates, and species that are particularly fecund. Those least successful in colonizing old fields were the dominant rainforest tree species and epiphytic ferns.

"The useful encourages itself; for the multitude produce it, and no one can dispense with it: the beautiful must be encouraged; for few can set it forth, and many need it."

J.W. von Goethe (1917). Wilhelm Meister's Apprenticeship, para 42, Book VIII, Chapter V, The Harvard Classics Shelf of Fiction. (http://www.bartleby.com/314/805.html)

Chapter 7 Final discussion

7.1 Abstract

This chapter integrates the results of the preceding chapters with existing literature and demonstrates that LC influence is an important determinant of the composition and successional trajectory of wet eucalypt forest. Historical landscape patterns are likely to have influenced the current distribution and abundance of plant species and their genetic diversity. Although there was evidence that landscapes at the time of disturbance are a particularly strong determinant of the successional trajectory for a site there is also evidence that an ongoing species turnover is influenced by changing patterns in the surrounding landscape. Plant characteristics such as longevity, seed banks and the capacity to resprout enable some species to persist at sites regardless of disturbance and their LC. Others which are more sensitive to disturbance severity or frequency may be lost unless suitable habitat is maintained in the surrounding landscape from which they can recolonize.

The question of whether rainforest, mature wet eucalypt forest and regrowth wet eucalypt forest may represent alternative stable states is examined in the light of the proposal that landscape traps may cause a switch in the steady state. In areas where the climate is marginal for the development of rainforest and mature wet eucalypt forest species, timber harvesting and any associated increase in the disturbance regime, including fire severity, may lead to a permanent elimination of rainforest species and mature forest habitats, consistent with the theory of a landscape trap. However, without a shift in climate, and in areas climatically and edaphically ideal for rainforest development, it is likely to be difficult to bring about a permanent shift in the steady vegetation caused only by the feedback between timber harvesting and fire severity and frequency. Nevertheless, there is strong evidence from this thesis that the capacity for mature forest species to recover from perturbation does decline as the abundance of mature forest habitat is reduced within the landscape. This evidence is consistent with the concept of a landscape trap. Measures to mitigate the impacts of timber harvesting and to increase the landscape resilience are provided.

7.2 Introduction

The primary purpose of this thesis is to evaluate the extent to which landscape context (LC) influences successional trajectories and spatial variation in assemblage variation and associated species distributions. Succession within forest is defined as any process that leads to the replacement of one plant species with another through time following exogenous disturbance (Horn 1974; Lienard et al. 2015). Few wet eucalypt forest sites have been the subject of any longitudinal studies. To my knowledge there are no longitudinal studies that trace the structural and floristic changes of wet eucalypt forest from the time of a disturbance through to the development of the community as a mixed forest. Therefore, understanding of wet eucalypt forest dynamics is still based largely on observed differences between communities of different times since fire, and changes at just a few sites observed over shorter periods (e.g. Gilbert 1959; Cremer and Mount 1965; Jackson 1968; Ashton 1981b; Brown and Podger 1982a; Hill and Read 1984; Hickey 1994; Ashton 2000; Serong and Lill 2008; Neyland and Jarman 2011; Turner et al. 2011).

The present discussion qualifies the conclusions from earlier chapters and re-evaluates the timing of floristic changes for pioneer and mature forest species in the context of other studies. The implications for biodiversity conservation at local and regional scales in the context of current forest management practices and climate change projections are considered, and measures that might mitigate adverse impacts from timber harvesting on LC and vascular plant biodiversity are suggested.

In particular this chapter discusses the hypothesis that wet eucalypt forest and mixed forest vegetation represent alternative stable states (Jackson 1968; Wood and Bowman 2012). If these vegetation types do represent alternative stable states rather than simply a successional continuum, it implies that environmental feedbacks maintain the distribution of these vegetation communities steady at least at temporal scale of a century or more. If so LC is likely to provide one of these feedbacks and may even contribute to the development of the type of landscape trap proposed by Lindenmayer et al. (2011). Lindenmayer et al. (2011) distinguished situations in which vegetation is so substantially altered across the landscape by disturbance (e.g. timber harvesting and/or frequent wildfire) that the ecological feedbacks that would

ordinarily ensure the pre-disturbance vegetation communities recover following disturbance become so weakened that they do not, and termed this a landscape trap. The trap being caused by a shift in vegetation which results in a new set of ecological feed backs that prevent the earlier communities re-establishing (Lindenmayer et al. 2011). If landscape traps exist, then switching large areas of vegetation to an early phase of secondary succession may reduce the capacity of wet eucalypt regrowth forest to develop old growth forest structures and assemblages, which include giant eucalypts and mature trees of primitive taxa such as *Anodopetalum biglandulosum*, *Eucryphia lucida* and *Nothofagus cunninghamii* in the understorey. The evidence from this thesis is used together with results from other studies to determine to what extent the alternative stable state model helps illuminate the dynamics of wet eucalypt forest successional dynamics and whether timber harvesting within the study area could lead to a permanent loss of mixed forest vegetation in the region if too much mature forest is replaced with single cohort stands of eucalypt regrowth forest.

7.3 Methodological limitations

7.3.1 Mapping precision

Mapping precision in the study region affected the reliability of estimates for total habitat area, distance to mature forest and fire history age classes. Inaccuracies in the mapping of the two dominant eucalypts and lack of mapped discrimination of understorey type limited the data that could be included in the present study, and will reduce the capacity of managers to undertake landscape planning. The results of the present thesis suggest that the discrimination of mixed forest communities from other vegetation is important for planning and managing biodiversity at the local and regional scales. The recommendation made previously by Lynch and Nelder (2000) that mixed forest communities be mapped separately in regional vegetation maps is endorsed. This discrimination has already occurred in most parts of Tasmania for some eucalypts (e.g. *Eucalyptus obliqua*), but remains an outstanding task in other areas and for other eucalypts. A possible approach for achieving this outcome is described briefly in Appendix 7.1.

7.3.2 Substrate variation and community composition

The concept of habitat is a critical component of landscape ecology (Fahrig 2013). Climatic and edaphic factors are strong determinants of community variation and species abundance within wet eucalypt forests and rainforests in the study region and across Tasmania (Kirkpatrick et al. 1988). Although sampling was confined to wet forest dominated by *Eucalyptus obliqua* and *E. regnans*, the sites sampled, and more particularly their landscapes, included a broad range of soils and climates. The metrics that described the LC surrounding each sample point were attributes of vegetation structure but did not describe other environmental attributes of the landscape important to the species compositions of the vegetation in the landscape such as climate and soil type etc. In the analysis of LC effects on species with broad ecological tolerances (e.g. *Nothofagus cunninghamii* and *Atherosperma moschatum*) this omission was likely not to impact on the effectiveness of these metrics (chapter 4). However, for species with a more restricted environmental range such as the hygrophilous rainforest species confined largely to acidic soils, such as *Anodopetalum biglandulosum* and *Eucryphia lucida*, the capacity to infer LC influence may have been reduced because the metrics used failed to provide a surrogate for the amount of mature forest situated in high rainfall areas with acid soils.

Determination of within site variation in species composition at 15 coupes in the study region enabled effects of LC to be distinguished for species groups (chapter 3). However, individual species analyses were more difficult due to the small number of ubiquitous species. Sampling sites restricted to one geological substrate and rainfall zone would have better assisted in discriminating the impacts peculiar to LC but failed in elucidating anything about the interaction between climate, soil and LC.

7.3.3 Correlation of climate, disturbance and LC

Bowman et al. (2015) observed that switches between vegetation states are only likely to occur when the environmental feedbacks that maintain vegetation stability are weakened. They recommended multi-faceted approaches to understanding ecosystem dynamics, including the identification of the parts of the system that are correlated and the relationships of these correlations to landscape-level feedbacks.

In the study region, as for Tasmania more generally, there is strong covariance between the major climatic gradient and the gradient in natural and anthropogenic disturbance regimes. This covariance reduced the capacity to distinguish landscape effects from climate and disturbance regime effects in the analysis of individual species (chapter 4) and species groups (chapter 5). By studying within site variation in species composition at 15 coupes, the effects of regional climatic variation were able to be better disentangled from other effects (chapter 3). Although it may have been possible to sample over a larger region in such a way to control for each of these separate effects within a replicated design, the logistical issues of access, transport and survey time would have increased. Furthermore, the reduced uniformity in other parameters would have led to more varied species pools, and reduced rather than improved the opportunity to analyse LC effects on individual species.

7.3.4 Autocorrelation among LC metrics

The variation in abundance of habitat types is strongly auto-correlated through both space and time, making it difficult to determine at what spatial and temporal scale species respond to LC. Opportunities to detect at what scale species and species groups were responding to LC were further hindered in the present study region by the sampling design (chapters 4 and 5). Over half of the plots were placed in parts of the study region that had similar disturbance levels for three scales of calculation (500 m, 1000 m and 2000 m radius). Although some autocorrelation between temporal and spatial scales is often encountered in landscape data (see chapter 2 Dormann et al. 2013) an even higher degree of auto-correlation between the temporal and spatial scales resulted from using this sampling design than might have been expected from more randomly located plots. The choice of method for the experimental forest landscape (EFL) project was justified on the basis that it was more likely to enable the detection of a response to LC among the greatest number of species, given an assumption that species vary greatly in their sensitivity to spatial scale of LC (Wiens 1992; Chust et al. 2004). Data were pooled from several project collections in order to reduce the impact of scale consistent LC sampling of the EFL data and to increase the power of analyses. Nevertheless, the lack of observed difference between the results for different spatial scales should not be interpreted as any indication that the relationship between species and its landscape is not scale-

dependent, due to the artificial increase in the correlation between scales that resulted from the sampling strategy.

The omission from consideration of LC effects other than the local effects of mature forest influence may also have obscured any potential effects of broader scale LC (chapter 3), but this was not the focus of the chapter.

7.4 Successional and disturbance dynamics

Time since disturbance was associated with both floristic composition and heterogeneity within wet eucalypt forest. Old growth forests had the least floristic variation between patches but the greatest within-patch floristic heterogeneity when sampled with 10 x 10 m plots and measured in terms of Bray-Curtis dissimilarity. Floristic variation within patches was least for the youngest regrowth forests. Age accounted for at least 16% of the patch-to-patch differences within the wet forest sampled in this thesis (Chapter 4). This effect of age led to an underestimation of age-related assemblage differences, since covariates that explained other aspects of the assemblage variation were also correlated with age, particularly soil chemical attributes (Ellis and Graley 1987). The age trend was also obscured by the impact of climatic, edaphic and fire regime differences, which accounted for a similar proportion of the variance in assemblages as age. Forest burnt only once since 1897 were more similar to old growth patches than patches of the same time since last disturbance but which had also been disturbed by fire between 1897 and the most recent disturbance event. This trend was most apparent among the regrowth forest with mature trees most recently burnt in the 1930s (data not shown).

Regrowth composition became increasingly similar to mature forest assemblages with increasing time since regeneration (chapter 3). Longitudinal studies spanning less than ten years immediately post-harvest have observed that forbs and graminoids are often the initial dominants but these are rapidly replaced in importance by ground ferns and taller tussock sedges, which, in turn, become overshadowed by woody plants within the first decade (Cremer and Mount 1965; Wapstra et al. 2003; Neyland and Jarman 2011). Many of the pioneer herbs in recently disturbed sites are rare or absent in mature forest communities (Murphy and Ough 1997). In contrast to the high cover

and richness of pioneer species establishing in the first decade, the frequency and cover of mature forest species is usually much lower within the same period (Cremer and Mount 1965; Wapstra et al. 2003; Neyland and Jarman 2011).

Even within the first three years, it is clear that the abundance of mature forest species varies greatly, depending on the type of forest present at the site prior to disturbance and the nature of the disturbance (Ashton 1981b; Neyland and Jarman 2011; Hindrum et al. 2012; Baker et al. 2013a). Data from the present study confirm that regeneration after harvesting mixed forest often has a higher establishment rate of mature forest species by resprouting than other harvested forest (Neyland and Jarman 2011; Baker et al. 2013a). Forests disturbed twice in one century had a much lower richness and cover of mature forest species than forests of the same age burnt only once. Many mature forest species are also more abundant after a single wildfire event than following clearfell and burn treatment, even when the vegetation prior to disturbance was mixed forest (Hickey 1994; Turner and Kirkpatrick 2009; Baker et al. 2013a). More details are provided about floristic variation in response to disturbance within Appendix 7.3.

A high dispersion within the mid-stage silvicultural class (24–28 years since regeneration) was observed in the present study (chapter 3). Further testing of a larger data set is needed to conclude whether variability in species turnover rates leads to greater floristic variability within and between patches in this age class, compared to others, or whether the weak result was simply an artefact of too few replicates.

Ashton (2000) provides the longest study of wet eucalypt forest, with a monitoring period approaching fifty years (see details in Appendix 7.3). Among the understorey dominants, there was a loss of many pioneer species, a decline in density of woody pioneer species and a corresponding increase in the abundance of woody species with relatively low light compensation points. These shade tolerant plants were already present in his study site at the commencement of monitoring when the vegetation varied between 25 and 50 years old. Ashton (2000) also observed that there was a shift in the dominance of the ground layer to species not reported in the initial assemblage. The increased density and cover of mature forest trees was achieved through growth of individual trees and some vegetative regeneration rather than

seedling recruitment. Seedling recruitment was uncommon but was observed for mature forest species and some pioneers in canopy gaps created by the senescence of understorey trees (see Appendix 7.3).

From the present study, it seems likely that understorey vegetation that remains undisturbed by fire for more than 100 years is dominated by woody species that colonized prior to canopy closure. However, the ground cover and epiphytic fern flora is less determined by early recruitment, and has a greater opportunity to change. Pioneer shrubs and herbs are able to recruit into canopy gaps in mature forest, and maintain a presence in mixed forest (e.g. *Pimelea* species, *Coprosma quadrifida* etc).

Although recruitment of woody species (of both pioneers and rainforest species) into forest understoreys may occasionally occur at any time after canopy closure, later arrivals will not result in rapid shifts in dominance. Low light levels will prevent most seedlings, even of rainforest trees, from establishing anywhere except in canopy gaps. On high nutrient sites, self-thinning results in the expansion of dominant individuals at the expense of suppressed plants of the same species, and may occur slowly enough to prevent the creation of light gaps. It is also likely that canopy expansion by already established neighbouring species will limit the size of light gaps created when cohorts of a common species reach the end of their life span (e.g. *Cassinia aculeata* ~20–30 years, *Acacia dealbata* 30–50 years, *Pomaderris apetala* ~90–120 years). On lower nutrient sites, *Gahnia grandis* occupies available light gaps. Canopy gaps in these forests mainly arise due to tree falls by mature eucalypts, and provide the main opportunity for colonization by new species into the patch. Hence, the successful establishment of species after canopy closure is slow and intermittent, and the low light conditions of the understorey ensure growth rates of new arrivals are slow.

7.5 LC effects on recolonization and succession in the first 50 years after disturbance

The primary focus of this thesis was to determine if LC was important in the recolonization of silvicultural areas following timber harvesting. This information increases understanding of the impacts of timber harvesting, and may enable the development of landscape management rules and harvesting techniques that might

mitigate these impacts. The study region provides an example of an intact forest region, within which mature forest has been fragmented by wildfire, timber harvesting and forest clearance. Variability in disturbance (including timing, frequency, size and intensity), has resulted in spatial and temporal variation in LC patterns in the regional vegetation (chapter 2). There was evidence within disturbance patches that richness and cover of mature forest species declined with distance from mature forest (chapter 3). This result extended beyond the patch-scale to the landscape, with many individual species (chapter 4) and richness and cover of floristic groups (chapter 5) demonstrating abundance patterns that were associated with LC. There was evidence from each of the chapters that differences in disturbance intensity affected the manner in which the vegetation responded to LC. This disturbance intensity effect was most apparent in the forest assemblages present on previously cleared land (chapter 6). Regrowth in old fields did not respond to LC as much as equivalent aged regrowth in areas that had not been previously cleared (chapter 6). The question remaining is whether these results demonstrate that LC may affect the successional trajectories of wet eucalypt forest?

The decline in mature forest species with distance from mature forest was already apparent in the first decade following regeneration (chapter 3). This patch-scale result is compelling evidence that mature forest influences the speed of the successional trajectory, particularly when considered alongside the results for older forests in the present study, and in the context of previously published results describing the variation in frequencies of rainforest species within patches (Tabor et al. 2007). Re-examination of data reported by Baker et al. (2013a) also demonstrated that the LC effect commences in the very first year following silvicultural regeneration (Appendix 7.2). In one year old regeneration, at sites near the boundary with unharvested and unburnt forest, richness of mature forest and other rainforest species varied from a mean of a half to three species, whereas the mean richness was always less than half a species in areas adjacent to forest that had been burnt (Appendix 7.2). Richness levels rose rapidly at the boundary and had reached ten to twelve in this species group within four to eight year old silvicultural regrowth (chapter 3), whereas at distances of 120 and 200 m the average was only between one and four in the same sized plots.

The observed LC effect in young forests is not restricted to the plants of Tasmania's wet eucalypt forests but extends to other regions of the world. For example, such a decline in mature forest species away from forest edges also occurs within the corresponding age class of silvicultural regrowth in the Douglas-fir forests of Washington State, USA (Baker et al. 2015). The trend in young regrowth apparent in the vegetation in the study region was also present in the beetle assemblages, but not in the frequency or richness of birds measured at the same sites as the present study (Hingston et al. 2014).

There was no trend in total richness of pioneer species across the 200 m distance gradient in the first decade of silvicultural regrowth. This result implies that the initial establishment of many pioneer species was not reduced in areas near mature forest, despite the low probability that this vegetation provided a significant propagule source. This pattern within patches has implications for understanding community dynamics and for successional trajectories. The lack of LC association observed in the initial establishment of plant pioneer species requires further investigation to determine if it extends to wet eucalypt sites where adjacent vegetation is young regrowth, and to other taxonomic groups such as beetles. The small number of young sites sampled for the present study reduces confidence in the result that initial colonization is not subject to patch-scale variation in LC. The study of initial pioneer establishment at a landscape-scale rather than only at the patch-scale would further determine if pioneer species are more independent of LC effects than mature forest taxa for their initial establishment. However, it seems likely this is the case, since a large number of pioneers do have good persistence (soil-stored seed bank and bradysporous species) or dispersal capacities (species with wind or vertebrate-dispersed seed) that, even at the landscape level, richness of pioneers in the decade immediately after disturbance will be less dependent on LC and more dependent on disturbance history and prior vegetation in the patch (Ashton 1981b).

Beyond the first decade, pioneer species developed a negative association with mature forest influence in older silvicultural regrowth patches. Successional processes near the mature forest edge resulted in a more rapid increase in cover and richness of mature forest species at the expense of both cover and richness of pioneer species. At locations far from mature forest, pioneer species richness and cover remained high. In

locations 200 m away from the edge, mature forest species, richness and cover increased more slowly than in areas nearer to mature forest. The cover of mature forest species increased even more slowly in areas more removed from the boundary. Differences in the sensitivity of the pioneer species groups are discussed in more detail in Appendix 7.3.1.

Although the Tasmanian wet eucalypt forest understoreys in the study region developed greater similarity to mature forest at the patch boundary adjacent to mature forest, assemblages throughout most silvicultural regrowth remained dominated by pioneer species for the first 45 years after regeneration, and floristic similarity to mature forest remained relatively low. In contrast, the plant assemblages in the Douglas-fir regrowth communities were already reaching high levels of similarity to adjacent forest after much shorter times following regeneration (Baker et al. 2015). In the silvicultural regrowth of the present study, the main rainforest canopy trees (*Atherosperma moschatum*, *Eucryphia lucida* and *Nothofagus cunninghamii*) are still very small compared with their size in mature forests, and even after reaching reproductive maturity, are likely to provide only a small propagule source compared with trees in mature forest patches. The quality of mature forest patches, measured in terms of the abundance of mature forest species in the understorey, was positively associated with an increased abundance and richness of mature forest species within silvicultural regrowth (chapter 3). This result suggests that silvicultural regrowth patches, which generally have a very much lower abundance of mature forest species than mature forest patches, will not have the capacity to positively influence the recovery of mature forest species in adjacent areas that have been more recently harvested, at least until such time as the rainforest trees have become dominant in the understorey.

The results of chapters 4, 5 and 6 demonstrated that the species abundance and assemblage variation responses to LC variation are not restricted to the patch scale but extend to landscape-level variation, and have implications for local and regional level conservation management. The contrasting result that assemblages in old field secondary regrowth forest do not show any association with their LC provides an example that LC influence does not over-ride disturbance impacts and other environmental limits to species distributions. The distinctive assemblages present in

old field sites compared with uncleared forest are examples of alternative trajectories in the succession of wet forest. Matching areas of non-cleared forest in the vicinity of old field regrowth displayed an association with LC metrics which was consistent with the results of chapter 5, demonstrating that the lack of association with LC metrics in assemblages in regrowth on old field sites was not due to climatic or substrate differences. The limit in mature forest influence is more marked in areas where disturbance frequency is higher. In areas burnt more than once in a century, re-establishment of mature forest species was much more confined to the mature forest edge (chapter 4).

The individual modelling of species abundance (chapter 4) and pioneer and mature forest species group modelling (chapter 3, chapter 5) all demonstrated that there were fundamental environmental restrictions on plant species distributions that impact on possible trajectories of wet eucalypt forest. These restrictions will limit the capacity for remnant mature forest patches to influence either the establishment of mature forest species or the trajectories of regrowth forest succession. The issue of distribution limits requires addressing before consideration of alternative stable state models and mitigation measures for timber harvesting can be addressed.

Given the issues of environmental variation on the relative influence of mature forest, it would be expedient in future to control more carefully this variation in site selection, or to undertake an experimental approach to harvesting operations so as to generate paired areas of similar environment but different distances from mature forest.

7.6 LC effects in forest more than 50 years after disturbance

To meet sustainable management objectives within timber production regions, mature forest patches will need to be maintained to ensure the protection of late-stage species that are poorly represented in silvicultural regrowth. However, without adequate protection buffers against impact from the edge effects due to disturbance in surrounding landscapes, the value for biodiversity conservation derived from mature forest reserves will be reduced (Kelly and Rotenberry 1993; Lindenmayer et al. 2013a). The tendency to-date has been to rely on the state-wide and regional

Comprehensive Adequate and Representative reserve (CAR) network which includes informal reserves (e.g. stream-side reserves) to protect biodiversity values within the timber production regions. Accompanying this practice is the hope that these reserves, no matter what size, will provide viable habitat for maintaining harvest sensitive species including mature forest plants regardless of the LC surrounding these reserved areas. Developing a better knowledge of how LC is likely to impact on biota within mature forest patches is important for sustainable forest management. However, this was only a minor focus of the present study of LC effects.

Studies within mature forest patches have demonstrated that impacts from adjacent vegetation is most evident at the edge of the patch and that the depth of edge effects varies greatly depending on several factors including adjacent land use or vegetation, the structure and composition of the forest vegetation, the time since the edge was created and the aspect of the edge (Westphalen 2003; Matlack 1994b). It is also highly variable depending on the response variable being measured (David Lindenmayer personal communication, October 2016). For example to protect mature hollow bearing trees in Victorian *Eucalyptus regnans* forest, a critical habitat component for Leadbeater's possum, Lindenmayer et al. (2013a) recommended buffers of 100 m because harvesting at distances closer than this is associated with a higher rate of collapse in these trees (Lindenmayer et al. 1997). In contrast, Westphalen (2003) found that timber harvesting affected the microclimate and epiphytic flora of wet eucalypt forests for a distance of only ten metres into the patch from the edge of harvest sites, and that these effects lasted for at least 15 years. Baker et al. (2014) observe that the mature forests of the present study (chapter 3) that were adjacent to regrowth less than ten years since regeneration, had greater microclimatic variability when compared with mature forest remnants adjacent to older regrowth, demonstrating that there was a decline in the edge effect with time, however climate stations were measured at 15 and 35 m in from the edge and suggest that micro-climatic effects due to adjacent harvesting may extend beyond the 10 m estimated by Westphalen (2003). However confounding the results observed by Baker et al. (2014) was their observation that canopies of the mature forest patches adjacent to the youngest regrowth patches were less dense, a factor which may have been a random difference in sites sampled rather than an effect of recent harvest and change in

microclimatic variation. Longitudinal monitoring of the climates in these remnants might assist in determining the relationships between these factors.

Other important impacts on mature wet eucalypt forest and rainforest from adjacent timber harvesting in Tasmania include the increased likelihood of damage from wind-thrown trees extending more than 50 m into the stand (Westphalen 2003; Neyland and Brown 1994). Such effects were observed during this study and also resulted in the exclusion of some sites from investigation. Among the indirect effects of physical damage by both wind-thrown trees and other mechanical damage resulting from timber harvesting and new road and fire break construction is a substantially increased mortality of mature trees of *Nothofagus cunninghamii* in mixed forest and rainforest stands resulting from myrtle wilt, a disease cause by the native fungus *Chalara australis*, (Packham 1991). In some areas up to 70% of the canopy trees have been killed by myrtle wilt along road edges. Increased mortality rates in mature trees can occur for distances of 200 m from road works and persist for many years. In order to protect myrtle stands from myrtle wilt buffers of between 50 and 250 m width have been proposed (Kile et al. 1989). A more conservative estimate of a 350 m buffer for high risk area has also been proposed (Packham 1991). In contrast to these suggestions, Neyland and Brown (1994) recommended that an adequate buffer for protection of most relict rainforest patches in eastern Tasmania from harvesting operations was 40 m. Packham (1991) listed some of the risk factors for myrtle wilt including: density of *N. cunninghamii* (highest dense stands of *N. cunninghamii*), average size of *N. cunninghamii* (highest for stands with large old trees), forest type (higher for mixed forest with callidendrous rainforest understoreys) and altitude (highest for lowland areas). Dead trees of *N. cunninghamii*, which had probably been killed by myrtle wilt were observed in mature forests in the current study in both remote areas of the study region and in areas adjacent to harvest areas but no analysis of the distribution of this mortality was undertaken.

Evidence from intensive studies elsewhere has also demonstrated that fragmentation has major impacts on tropical forests (Laurance et al. 1998b; Laurance et al. 2006). Recruitment and mortality rates were greatly affected by fragmentation, particularly within 100 m of forest margins (Laurance et al. 1998b; Laurance et al. 2006). Rare, uncommon and old growth taxa were most vulnerable to losses due to fragmentation

(Laurance et al. 1999; Laurance et al. 2006). Matlack (1994b) reported that the distribution of herbs in Pennsylvanian forest understoreys was associated with distance from edges and that some trace of this pattern was still evident even when adjacent areas had been reforested for more than 55 years. The only other comparable studies for vascular plants in Australian eucalypt forests, to my knowledge, are from the Tumut experimental fragmentation site at Wog Wog, New South Wales (Farmilo et al. 2014; Morgan and Farmilo 2012). In that area there has been a general increase in the abundance of common plants and the density of some species has increased preferentially in the smallest remnants (Farmilo et al. 2014; Morgan and Farmilo 2012).

The present study did not investigate patterns of species distributions and richness in a manner that could reveal whether patch size or time since fragmentation resulted in any changes in the abundance of common species or losses in species richness and rare species, although the data already collected has the potential to be analysed in this way. The present study did demonstrate that there were associations with LC measured at scales of 500 m to 1 km in the abundance of common species within mature forests (Table 4-5, Appendix 4-10). Assemblages in mature forests although not associated with current year LCI scores, were associated with the historical landscape context scores (Table 5-3). The individual modelling of plant species in regrowth forest plots which included both silvicultural regrowth and wildfire regrowth between 70 to 110 years since last burnt provided similar results as those of silvicultural regrowth forest on their own, demonstrating the patterns in response were no less strong in older regrowth classes. Models of individual species abundance within mature forest plots, when separately analysed, demonstrated that nearly half of the common plant species in these forests showed clear patterns of association with LC, including both positive and negative associations.

Two thirds of the associations between species abundance and LC were strongest for LC metrics generated for historical landscapes. The selection of current year landscape metrics in the models may be a product of the high correlation between historical and current LC patterns. It is therefore possible that the observed associations between the abundance of species and LC in mature forest patches is due to the lasting impact of historical LC patterns on the stand development, rather than a

response to mature forest habitat losses in surrounding landscapes caused by timber harvesting over the last 50 years. However, the alternative explanation is that some pioneer species are more likely to colonize disturbance gaps in mature forest surrounded by young regrowth forest which is providing a greater source of propagules than would be present in mature forests in less disturbed landscapes. These pioneer species may be able to colonize at the expense of rarer later stage species.

Since fragmentation may lead to changes within remnant forest communities, more research at the local patch scale in mature forest, including longitudinal studies, is warranted to evaluate further the capacity of mature forest and rainforest remnants to provide secure protection for late stage species, especially less common taxa.

7.7 Limits to rainforest and mixed forest distributions

In Australia *Nothofagus cunninghamii* is mainly distributed in areas with reliable summer rainfall with a mean annual precipitation of more than 1500 mm (Read and Brown 1996; Lindenmayer et al. 2000a). In Tasmania this is equivalent to about 250 mm in the warmest quarter, or 80 mm in the driest month (data calculated from BIOCLIM layer, Landscape Logic 2008). In lower rainfall areas, *N. cunninghamii* and other rainforest species are generally restricted to areas where ground water provides an additional moisture supply or atmospheric humidity is high due to mist or topographic shelter (e.g. gullies). However, as there is a strong correlation between warm-dry climates and higher disturbance frequencies, it is unclear whether it is climate or disturbance which is limiting the distribution of *N. cunninghamii* dominated rainforests (Read and Busby 1990; Read and Brown 1996).

Within the silvicultural regrowth in the study area, average levels of mature forest species cover, richness and dissimilarity to mature forest were predicted at about this same threshold in rainfall (Appendix 3.2.2.1: Figure 3-F). Hence these species do regularly extend into the warmer drier areas, but are progressively less common as rainfall levels reduce and temperatures increase.

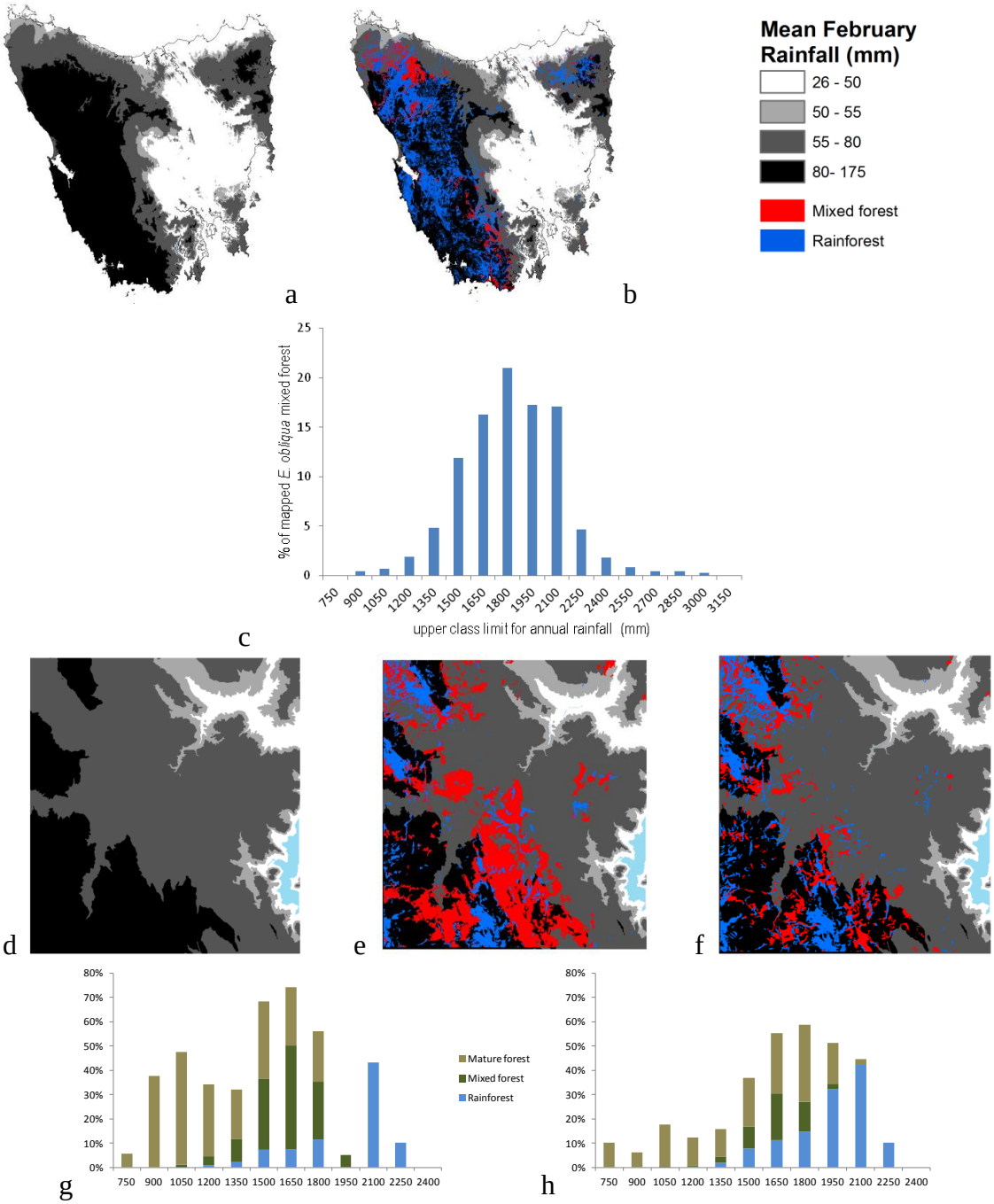


Figure 7-1. Rainfall distribution in Tasmania (Landscape Logic 2008) (a), distribution of *Nothofagus cunninghamii* rainforest and *Eucalyptus obliqua* mixed forest (DPIPWE 2013) (b); the percentage area of *E. obliqua* mixed forests by rainfall classes (c) rainfall distribution in the study area (d), distribution of rainforest and mixed forest in 1947 (e) and 2009 (f); and the proportion of each rainfall class in the study area occupied by rainforest, mixed forest and other mature forest in 1947 (g) and 2009 (h).

The general absence of both *Nothofagus cunninghamii* and *Atherosperma moschatum* and dominance of understoreys by *Olearia argophylla* in areas such as the central highlands of Victoria is likely to be due to their low rainfall (Ashton 1981b, 2000).

Ashton (1981b) hypothesised that this community represents a climax vegetation that would remain stable through time in relatively low rainfall areas, but he noted that due to their lower rainfall these areas would be less likely to remain unburnt for long enough to demonstrate such stability. In fire-protected refugia in eastern areas of Tasmania, dry rainforest communities co-dominated by *Olearia argophylla*, *Pomaderris apetala* and other species are widely distributed (Pollard 2007), providing support for his hypothesis.

7.8 Temporal effects of landscape context

Mature *Nothofagus*-dominated rainforest has a cool moist microclimate, which usually ensures that it is unable to burn at most times of the year (Jackson 1968; Styger 2014). Rainforest is only able to sustain fire at times of the year when the total rainfall in the preceding month has been less than 50 mm (Styger 2014). Given this, it is not surprising that rainforest vegetation (including mixed forest) is almost completely absent from areas with a mean monthly rainfall for the driest month of below 50 mm (Figure 7-1). The variability of summer monthly rainfalls also strongly influences the distribution of rainforest (and mixed forest), since any areas with a reasonable chance of experiencing rainfall below 50 mm in a 30 day period are vulnerable to fire at sufficient frequencies at the century to millennial time-scale to exclude poorly dispersed rainforest species such as *Nothofagus cunninghamii*.

The hypothesis posed in chapter 5, that LC at the time of disturbance is more important in determining the successional trajectory of the communities in wet eucalypt forest than current LC, was only partially supported. Given the absence of good evidence, a narrative based on the available evidence is provided which describes likely variation in LC influence over the successional cycle of a forest patch (Appendix 7.5).

One of the major mechanisms of LC influence on plant communities is the regulation of propagule availability. When LC is more broadly defined to include the pre-disturbance vegetation, then it becomes clear that LC is the strongest determinant of the composition of forest patches following disturbance. Regardless of the definition, the capacity of LC to influence the composition of wet eucalypt forest patches is

constrained by the dispersal and persistence capacity of individual species and their ecological tolerance. Since light regulates the capacity of many species to regenerate within wet forest patches (Ashton and Turner 1979), following canopy closure it is likely that canopy density and competition from established plants for light provide major forces of resistance to LC influence. Regenerating vegetatively can overcome shade intolerance to a certain extent, but requires that plants already be established within the patch (Read and Hill 1985b; Ashton 2000).Therefore, as Ashton (2000) observed, the rate and the trajectory of succession of woody plants within the understorey for at least fifty years in the absence of further disturbance, may be predicted on the basis of shade tolerance, relative growth rates and life spans of the tree species that established in the patch at canopy closure. In areas climatically suited to the establishment of mixed forest where propagule sources are available the majority of woody understorey plants that will be important in the later successional forest at the site will arrive soon after disturbance. Most rainforest species, although present in many areas soon after disturbance only begin to become important in the patch more than seventy years later, a situation best fitting the tolerance pathway by Connell and Slatyer (1977). However, there was also evidence from this thesis that mechanisms of competitive exclusion (Tilman 1990) may be operating so that the pioneers are excluded in areas close to mature forest, while in situations where *Pomaderris apetala* establishes in fertile situations, the importance of *Nothofagus cunninghamii* and successional rate to achieve mixed forest is reduced.

The much later arrival of the epiphytic flora, and other late-stage species, which may be important in older forests, is in keeping with the facilitation pathway (Connell and Slatyer 1977). Suitable micro-climates and substrates limit the arrival of these species, but the results of this thesis also demonstrate that the arrival of these species is affected by LC. Therefore, LC has a much reduced but continuing influence on stand composition after canopy closure. Species such as epiphytic ferns will have a higher chance of colonizing where substrates are available and mature forest is abundant in the landscape (chapter 3, chapter 4, chapter 5). It is likely also that the patch will be colonized by rarer species where such species are located in nearby forests. Fragmentation of the patch (e.g. the replacement of some areas with younger regrowth forests) will create edge effects and increasing abundance of young regrowth forest in

the landscape will increase the likelihood of pioneer species establishing in disturbance gaps and margins of the patch at the expense of more specialised late stage species (Appendix 7.5).

The current study was limited in its scope to the examination of temporal effects of LC at the decade to century scale. It was also largely restricted in its examination to the effect of LC on alpha diversity in plants. Yet it is likely that LC influences plant distributions by influencing local species extinction events and geographic range expansion at the century to millennia scale, within the confines imposed by the fundamental niche of each species. Isolation between potentially suitable environments is likely to prevent many species occupying their potential environmental niche. In a preliminary analysis of Tasmanian and Victorian data for wet forest communities of *Eucalyptus regnans* (Kirkpatrick et al. 1988), not hitherto reported in this thesis, the beta diversity of these communities was found to be lowest in northeastern Tasmania, to an extent not explicable by climatic and edaphic differences. This result and the absence of a substantial number of common palaeoendemic rainforest plants (*Anodopetalum, Anopterus, Archeria, Cenarrhenes, Eucryphia, Prionotes* etc) from this entire region suggest the possibility that past climate change (e.g. Pleistocene glaciations) may have resulted in such severe fragmentation and restriction of rainforest and wet forest vegetation that it has led to reduced levels of diversity. Climate modelling for palaeoendemic species, for which there was some evidence of under-prediction, does suggest that there is at least some areas of suitable climate in this region (Dr Greg Jordan personal communication 5th of June 2015). Genetic studies of both *E. regnans* and *Nothofagus cunninghamii*, demonstrate that they survived the last glacial period in isolated local micro-refugia within northeast Tasmania from which they were able to disperse when the climate became more suitable (Worth et al. 2009; Nevill et al. 2010). Although these data may suggest that these two species are relatively resilient to range contractions and climate shifts, there are relict rainforest patches in which *Nothofagus cunninghamii* is absent and the better dispersed tree *Atherosperma moschatum* dominates. The poor dispersal capacity of *N. cunninghamii* has also been mooted as a contributing cause for its absence from high rainfall areas of eastern Victoria (Read and Brown 1996). Although some degree of serendipity is probable, the limited dispersal of both

N. cunninghamii and *E. regnans* renders them more vulnerable to local extinction in isolated areas. Forest management ensures the replacement of *E. regnans* from harvest areas, but so far makes no attempt to re-establish *Nothofagus cunninghamii* or other understorey species within harvest areas.

Further studies of LC in which historical and current LC are very different are needed to further test this theory. However, the implication is that current population levels of rainforest species are strongly affected by the levels of mature forest in landscapes when each patch was harvested. The regeneration of future stands is likely to result in the return of the lower population levels of some rainforest species if the total habitat area of mature forest is lower. Some rainforest species may be locally lost from patches where climates are suited to the development of mixed forest but which are remote from mature forest stands after they are harvested. To ensure that future harvested areas have the potential to develop as mixed forest, mature forest habitats need to be maintained throughout the natural range of mixed forest, and silvicultural management techniques other than clearfell and burn considered where there are rare species or other special values to protect.

7.9 Are mixed forests and wet sclerophyll forest alternative stable states?

There is good evidence that buttongrass moorland and forest, especially rainforest vegetation, represent alternative stable states within the low fertility environments of southwest Tasmania (Jackson 1968; Wood et al. 2011; Wood and Bowman 2012; Fletcher et al. 2014; Bowman et al. 2015). The occurrence of shifts between vegetation states has been demonstrated in Tasmania, at least for low fertility soils (Podger et al. 1988; di Folco and Kirkpatrick 2013; Fletcher et al. 2014). What causes these shifts remains unclear. What is also uncertain is whether there is a basin of attraction that maintains areas of mixed forest separate from both rainforest and other wet eucalypt forest (Figure 7–2), either within the infertile zone of western Tasmania or the more fertile substrates of the Southern Forests within rainfalls that vary between 1000 to 2000 mm (Figure 7–2).

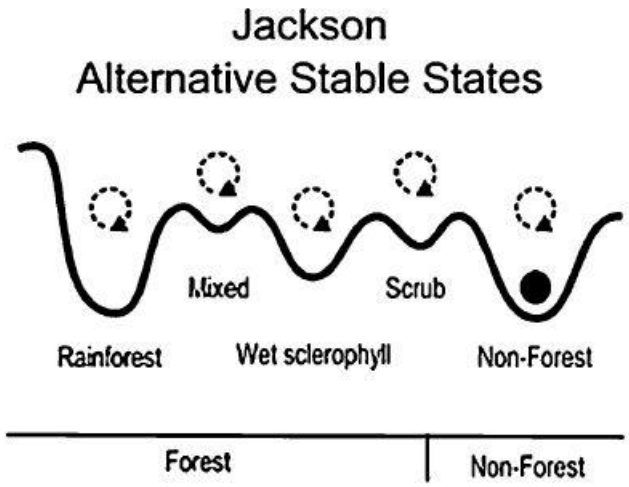


Figure 7-2. Part of diagram from Figure 1, Wood and Bowman (2012) illustrating the model of vegetation dynamics for southwest Tasmania proposed by Jackson (1968) presented within the framework of alternative stable states.

It demonstrates that although any vegetation community can occupy any underlying part of the physical environment (climate and substrate), once a vegetation type is established at a site, feedbacks between the vegetation and the environment create barriers to the shift between vegetation types. The relative stability of vegetation, i.e. strength of feedbacks maintaining the vegetation type, is indicated by the relative depth of the basins (cups). In their diagram, Wood and Bowman (2012) indicate the existence of significant barriers to the shift of vegetation from wet sclerophyll forest to mixed forest but that the feedbacks holding mixed forest in place through time are weaker, enabling vegetation to shift more easily from mixed forest to either rainforest or wet sclerophyll vegetation.

A basin of attraction that maintains moderately stable boundaries between mixed forest, other wet eucalypt forest and dry sclerophyll forest seems likely. Such stability has been reported for dry sclerophyll, wet sclerophyll and rainforest boundaries in fertile areas of the New England Tableland (Knox and Clarke 2012) and also between the tropical rainforest and savannah vegetation in the wet tropics of Queensland (Warman and Moles 2009). Knox and Clarke (2012) demonstrate markedly different fire and temperature regimes for each vegetation type. Importantly, they observe that more recently burned wet sclerophyll forest was more likely to burn with extreme severity than long unburnt wet sclerophyll forests, but that this was not true for rainforest. Fuel loads after six years did not differ between forest types or fire severity but temperatures were warmer in more severely burnt forest enabling greater drying of fuel beds, thereby increasing the probability of fire. There was no evidence that stand composition shifted towards more flammable assemblages following fire, even in severely burnt sites, although there were more short-lived fire-cued species in the

recolonizing communities. Within burnt rainforest many individual plants resprouted, an observation supported by response of rainforest species to wildfire in Tasmania (Barker 1991; Hill and Read 1984). Hence, they found strong evidence for stability of boundaries, and evidence for environmental and pyric-feed backs between the vegetation types, but no evidence that severe fire triggered a change to an alternate state.

The account by Knox and Clarke (2012), provides important evidence for stability, although their example does not include an account of vegetation described here as mixed forest, which is so extensive in Tasmania but is rare in warmer areas of Australia. Furthermore the case they describe is within a region with natural fire regimes, rather than one in which logging followed by burning dominates disturbance events. Tng et al. (2014) describe the distribution of tropical mixed forest dominated by *Eucalyptus grandis* in northern New South Wales and Queensland, which form a narrow belt of vegetation between savannah and tropical rainforest. Like the mixed forests in Tasmania, it is dependent on high rainfall and an appropriate fire regime to support the co-existence of both eucalypts and rainforest species (Tng et al. 2014).

Tng et al. (2014) suggest that both mixed forest and earlier successional stages of wet eucalypt forest represent unstable states within a basin of attraction to rainforest and should be managed as rainforest. They argue this on the basis of evidence by Tng et al. (2013) who found that the communities dominated by giant eucalypts in both the wet tropics and Tasmania occupy an environment common to rainforest, and that the plants of the rainforest and the plants of early phases in succession of wet sclerophyll forest share many traits in common, and which were distinct from the plants of savannah or dry eucalypt forest. Their interpretation of the available evidence appears to be at odds with models proposed by Jackson (1968) and Wood and Bowman (2012), and seems not to consider the widespread spatial and temporal stability of wet eucalypt forests within the palaeo records (Macphail 1979; Jackson 1999a). Once established, the long life span of eucalypts make it likely that fire will ensure their perpetuation in all but the most fire protected areas or infertile areas (Jackson 1968; Wood et al. 2010). In contrast to their interpretation, their data suggests that wet eucalypt forest forms an alternate stable state to rainforest, since they are vegetation communities with plant traits that enable them to occupy the same environments. The

question remaining is whether the vegetation in which mixed forest will develop are spatially stable and distinct from those that will not, or whether these two forms represent temporally unstable states within the basin of attraction of wet eucalypt forest.

If a basin of attraction exists for mixed forest vegetation within the present study area, the results of this thesis suggest that it is likely to be strongly controlled by climate and the disturbance regimes associated with climate and topography. In high rainfall areas mixed forest will be restricted to areas burnt frequently enough to maintain the eucalypts but not so often that rainforest species are eliminated (mean consecutive intervals between fires~150–350 years). In areas below 1500 mm it is likely that mixed forest will be largely restricted to areas which afford topographic protection from fire and drought (Jackson 1968, Wood et al 2011).

This hypothesis should be testable with better mapping, although artificial disturbance from timber harvesting would need to be accounted for. The existence of correlations between recovery rates of mature forest species and at least twelve environmental variables have been identified by the present study as possible evidence for feedbacks that could reinforce the re-establishment of mixed forest communities in areas where it previously occupied (Appendix 7.6). These factors may contribute to a natural separation across the landscape of these two forest communities, and which probably ensure moderately stable boundaries when measured over centuries.

The slow dispersal of the main canopy and understorey dominants of mixed forest and the widespread occurrence of mixed forest juxtaposed to wet sclerophyll communities and rainforest within the study region all contribute weight to the probability that their distribution is relatively stable through time, and may be usefully explored within the framework of alternative stable states. However, the results of this thesis also support, the notion illustrated by Wood and Bowman (2012) of Jackson's (1968) model, that mixed forest is likely to be less stable than wet sclerophyll forest. This instability arises as a result of the time required to achieve mature mixed forest vegetation and their sensitivity to disturbance interval.

Lindenmayer et al. (2011) have proposed the possibility that the recent increase in the frequency of landscape scale fires in Victoria is evidence of a landscape trap that has been triggered by the conversion following timber harvesting of large areas of mature wet eucalypt forest to regrowth. They argue that changing the demographic structure of the forests across a large area has resulted in increased continuity of highly flammable vegetation. They suggest that this increase propagates the loss of mature forests areas.

Attiwill et al. (2014) found no evidence that fire severity was related to the age of the vegetation, or whether it had been harvested or not. They argued that clearfell, burn and sow removes logging slash, which would otherwise contribute to extreme fuel loads post-harvest, and has achieved a substantial reduction in wildfires since its introduction. Some measurements of fuels in wet forest prior to logging, post logging and post burning have demonstrated that: pre-logging fine fuel loads vary greatly between forest types with some rainforest understoreys having much lower fine fuel loads (~13 t/ha) than those with wet sclerophyll species in the understorey (~20 t/ha); the slash from logging leads to much higher fuel-loads post-harvest (~40-85 t/ha); and the intensity of the regeneration fire determines the extent to which the fuel loads are consumed with intense fires removing the majority, whereas a low intensity regeneration burn may only consume between 50-90% of fine fuels depending on their moisture content at the time of the fire (Slijepcevic and Marsden-Smedley 2002; Marsden-Smedley and Slijepcevic 2001). Nevertheless, in support of the claim by Attiwill et al. (2014) that clear-fell harvesting reduces wildfire risks, at least in comparison with earlier harvesting practices, there have been no landscape scale fires in the wet forest regions of Tasmania since the introduction and widespread application of clear-felling.

On catastrophic fire days that coincide with less than 50 mm of rainfall in the previous month, all vegetation types are likely to burn. The distributions of fires and different degrees of fire severity will be driven by weather, topography and chance. However, as demonstrated by Jackson (1968) and Knox and Clarke (2012), natural vegetation distributions are not driven by single catastrophic fire events, but by the probabilities of fire events over millennia. Taylor et al. (2014) have demonstrated that fire severity is not linear with fire weather but was strongly associated with stand age.

Silvicultural regrowth forest between 7 and 40 years of age were more likely to be severely affected by wildfires than younger or older forest classes. Contributing to the greater impact of fire on tree survival in these forests include: the high fine fuel loads that result from the self-thinning of the eucalypts as trees develop and compete for canopy dominance (Ashton 1976; Taylor et al. 2014); the greater impact of ground fires on the canopy of trees due to their relatively lower height compared with mature trees (Mackey et al. 2002; Taylor et al. 2014); floristic differences such as a reduced abundance of tree ferns, rainforest species and moisture holding species such as bryophytes and epiphytic ferns may result in warmer, drier microclimates in the understorey and lower fuel moisture contents (Taylor et al. 2014; Wood et al. 2014). The high mortality is compounded by a lack of seed for regeneration since the reproductive age of *Eucalyptus regnans* is 20 years (Mackey et al. 2002) and the chances of seed survival is likely to be reduced when the canopy is burnt or scorched. Hence there is a higher probability of regeneration failure and conversion to other communities following wildfire in silvicultural forests between 7 and 40 years of age. The existence of stable states is predicated on there being resistance to shifts in vegetation between states. Lindenmayer et al. (2011) suggest that a permanent shift may have occurred for Victoria, although they do not provide irrefutable evidence of such a permanent shift.

In the long term, the distribution of communities is dictated by the probabilities of wildfire. This increases where stand structure results in warmer, drier microclimates. Baker et al. (2014) demonstrate that within the sites studied for this thesis, younger regrowth forests have more variable microclimates and warmer, less humid air than their mature forest counterparts, and that their fuel loads are likely to be drier in summer. Therefore there are more days in which young regrowth forests are able to burn than the number of days in which mature forest can burn (Jackson 1968). Litter loads, which are the main biological driver of fire fronts in these forests (Cheyney 1996), are highest in *E. regnans* forests between 35-45 years following regeneration (Ashton 1975b). Nevertheless the probability of fires burning young regrowth forest when mature forest will not burn are likely to progressively decrease as rainfall declines and temperatures increase. Topography and macro-climate will be a greater determinant of fire probability than the micro-climate and vegetation structure.

The presence of extensive road networks, reduced fuel loads in harvested coupes, and the policy of controlling fires will limit most fire events to the most extreme fire weather days, when fire control is impossible, and the chances of burning mixed forest will be high. Hence the study area is likely not to be subject to natural fire regimes, and those that do occur and get away are likely to be on catastrophic days when everything will burn. There is therefore no reason to think that a change in fire regimes due to timber harvesting will be responsible for a switch in permanent steady states in these communities, while the present forest management policies continue to operate. Of course reduced resources for fire management (e.g. in response to the reduction in size of the Forestry Tasmania), increased public access to the production forests (increasing the opportunity of accidental fires and arson), or changes in fire practices in adjacent areas (e.g. the reinstatement of the use of campfires, and experiments with burning practices in the Tasmanian Wilderness World Heritage Area) could all lead to increased fire frequencies. If this resulted then one might expect disturbance feedbacks to exclude rainforest species from fire prone sites, and in areas continuously vegetated by more flammable regrowth forest, larger fires may be more likely to burn into the edges of mature forests than if there had been a less continuous fuel load (Covington and Moore 1994a; Hessburg et al. 2000).

Climate change could be leading to the range contraction of *Nothofagus cunninghamii* and other rainforest species (Leao 2014; Worth et al. 2015), and this range reduction will be most evident following disturbance, as with the loss of rainforest species from the Wallaby Creek catchment after the Victorian 2009 fires. Summer rainfall is predicted to become reduced in western areas of Tasmania, while drought events are likely to increase (Grose et al. 2010; Grose et al. 2013; Grose et al. 2014). Recent modelling of Tasmanian forest fire weather danger predicted that increases in maximum temperatures in Tasmania are likely to result in an increase in frequency of extreme fire danger weather, although such events are naturally variable making change difficult to detect (Grose et al. 2014).

Due to the strong influence of LC and previous vegetation in the re-establishment of species at a site following disturbance, changes in species distribution patterns are likely to occur only slowly through time. The exception to this generalisation is where disturbance is severe enough to eliminate disturbance-sensitive species and change the

site conditions. Evidence from western Tasmania demonstrates that for low fertility environments, and even when fire is excluded, it is difficult for some forest species to expand their range (Brown and Podger 1982a; Brown et al. 2002; Wood and Bowman 2012). In these studies the conversion of buttongrass over 60 years to scrub or forest was largely restricted to areas within 40 m of a forest boundary, and in some cases was only precipitated by burning, which served to trigger seed release and establish bare ground for seedlings to establish (Brown and Podger 1982a; Brown et al. 2002; Wood and Bowman 2012). Whereas rainforest species would normally resprout after fire when rainforest or mixed forest is burnt but wildfire, following timber harvesting these species are much more dependent on sources of seed in the surrounding landscape for their reestablishment. Evidence from the present thesis suggests that if rainforest species are eliminated from local areas, those with short dispersal distances such as *Nothofagus cunninghamii* and *Eucryphia lucida* may be unable to regain their former range for long periods of time, possibly centuries, given migration rates estimated from this study of between 10 to 40 m per decade. These species are keystones of rainforest and mixed forest habitat upon which many other less common plant and animal species are dependent.

7.10 Implications for silviculture and forest management

In recent decades, there has been an emphasis on improving outcomes for the protection and conservation of biodiversity within regions managed for timber production (Hickey et al. 2001; Baker and Read 2011; Gustafsson et al. 2012; Baker et al. 2015). In Tasmania, changes that have already been adopted for the management of State forest areas include: no further conversion of native forest to plantation or non-forest; reduction in size and aggregation of harvest sites, the maintenance of an extensive Comprehensive, Adequate and Representative (CAR) Forest Reserve Network, including both formal and informal reserves for the protection of special values; and a shift, where possible, from clear-cut operations to variable retention forestry methods (including aggregated retention), especially in old growth forest (Tasmania 2009; Anon 2011; Department of Agriculture 2015). The results of the present thesis confirm that all these measures are likely to provide some regional and local improvement in the outcomes for vascular plant species conservation.

Additional suggestions and qualifications for the application of these general principles are provided here for consideration by forest managers.

7.10.1 Formal and informal protection of mature forest and old growth habitat

Old growth forests are now rare globally and their is a growing threat to ecosystem function in response to the loss of large old trees (Lindenmayer et al. 2012). Trees of the size of mature *Eucalyptus regnans* and *E. obliqua* are also a globally rare phenomenon, are important for carbon stocks (Dean et al. 2012; Tng et al. 2012) and are a critical for a range of hollow dependent fauna (Lindenmayer et al. 2014a). Between about 14% and 18% of the study area is likely to be old growth eucalypt forest or rainforest (chapter 2), though better mapping is required to be more precise. Much higher proportions of mature forest occur in the adjacent region which has been dedicated for nature conservation rather than wood production. Within the study area, widespread conversion of wet forests to younger communities has already reduced populations of mature forest species and altered the demographic structure of these communities. If they do represent alternate stable states, then the imposition of artificial disturbance regimes could be weakening feedbacks which enable these communities to recover after disturbance. These communities have the richest diversity in rainforest understoreys, and include both common and regionally uncommon rainforest species, many of which are primitive or endemic to Tasmania. As the study area is likely to have included refugia for wet forest and rainforest taxa in the last glacial (Kirkpatrick and Fowler 1998) and includes areas at the edge of the climatic range of several rainforest taxa, this and other regions of the Southern Forest contribute to the maintenance of genetic diversity. As other researchers have already recommended (e.g. Lindenmayer 2014), the results of this work further support the call to end timber harvesting in old growth eucalypt forest and adopt landscape management practices that ensure an increase in the amount of oldgrowth forest in future landscapes. This recommendation is distinct from other recommendations in relation to the management of mature forest vegetation (i.e. any forest with mature eucalypt trees dominating). It should also be noted that much of the remaining old growth mixed forest and rainforest in the study area and elsewhere in Tasmania is

already contained within informal and formal reserves. Within the study area in 2009 only about 1300 ha of such forest types remained allocated for timber harvesting (Appendix 7.7).

Forestry Tasmania has recently advocated a minimum target of 11-22 % of mature forest habitat be retained across native wet eucalypt forest landscapes, defining landscape in terms of a 1 km radius (Wardlaw et al. 2012). In some areas abutting formal reserves and informal reserves the levels of protection would be much higher than the minimum target. Retention of 20% of mature forest across the landscape was based on the assumption that key mature forest taxa are usually able to re-establish in silvicultural coupes within a time frame of fifty years in areas where mature forest is within 500 m of the coupe. As the proportion of mature forest increases in the landscape, the average proximity to the nearest mature forest also increases. To ensure that on average most silvicultural forest patches is within a buffer distance of 500 m of mature forest, the minimum required level of forest within the landscape would need to be at least 20% (Wardlaw et al. 2012). The target of 20% contrasts with the recommendation by Lindenmayer et al. (2013a) that in Victoria, where oldgrowth forests form only about 3% of the *Eucalyptus regnans* forest area, that to enable the maintenance of tree hollows and the recovery of Leadbeater's possum at least 30% of the forests need to be oldgrowth. Given the probability of wildfires within protected as well as harvested areas this target requires at least 50% of these forests in Victoria to be set aside and protected from timber harvesting (David Lindenmayer, personal communication October 2015).

The results of this study provide evidence that mature forest plant species have only a limited opportunity to re-establish in the first fifty years in areas more than 150 m from mature forest. To ensure that silvicultural forest patches are usually within 150 m of mature forest much more than 20% of mature forest would need to be retained. It was also found that many mature forest species have other environmental constraints limiting their re-establishment. Therefore, the imposition of a 20% retention target across all landscapes, although designed to mitigate against the biodiversity losses, may nevertheless be delivered at the expense of harvesting in high conservation habitat such as old growth and fail in delivering on the objectives it was designed to achieve in some areas.

Given these considerations, it is suggested that rules be developed to ensure the protection of key habitats for key taxa. For example, for hollow-dependent fauna rather than the currently proposed '20% rule', that an 'average mature tree density' be set to ensure a minimum number of mature trees are retained within a one kilometre radius to protect these taxa. This switch may result in quite different outcomes, but would need to be guided by experts on these taxa, to ensure that the protection of mature trees is coincident with other important habitat requirements for such taxa. Mature trees are also subject to wind damage when surrounding forests are removed and planning to ensure protection of mature tree densities should only be undertaken where the risk of wind throw is low.

For vascular plants, the 20% rule may be appropriate as the minimum retention target across all landscapes if other protection measures are established such as no further logging in old growth forest. Not all areas of the current study area have sufficient remaining mature forest to achieve this target at this point in time, especially areas surrounding agricultural land, plantations and regions impacted by harvesting prior to 1960 (Figure 7–3). Passive restoration by excluding second rotations within some areas, could lead to increased areas of mature forest in these low LCI regions within the next few decades. There are also additional protection measures that could benefit rainforest species. In particular it is recommended that a map of the natural distribution of mixed forest be prepared as a special management layer. The design of harvest areas where pre-logging surveys demonstrate that the forest understorey is well represented by rainforest plant species, should ensure that planned coupe areas are largely within the 150 m of mature forest stand so that these species are able to re-establish again after logging, this is particularly important where slopes and aspects are likely to reduce the successful re-establishment of rainforest species (Åstrom et al. 2007). However, in areas that this study found to be more resilient to harvesting impacts it may be acceptable to increase the distance threshold for some parts of the harvest area up to 250 m from mature forest where slopes are gentle, aspects are southerly, rainfall is more than 250 mm in the warmest quarter or, as Tabor et al. (2007) demonstrated, where sites that are downhill and downwind of mature forest.

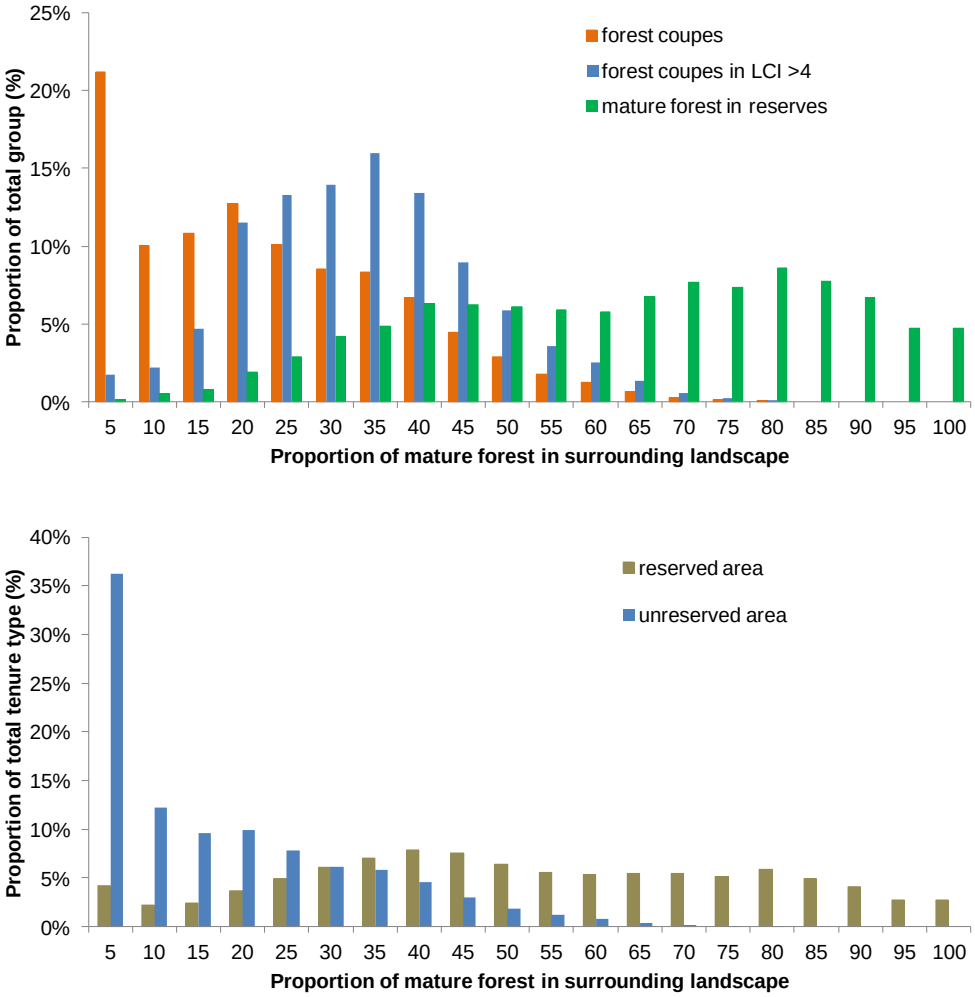


Figure 7-3. Proportion of total: forest coupes, forest coupes in Landscapes with an LCI of more than 4, mature forest in the CAR reserve system (above), total unreserved land, and total of land in the CAR reserve system (below)within each landscape category defined by the percentage of mature forest in the surrounding1 kilometre radius in 2009.

Note that 68% of unreserved parts of the study area have less than 30% of mature forest remaining in their surrounding 1 km radius, but much of this is in private land tenures. Likewise, although much of the native forest allocated to coupes had low levels of mature forest in surrounding areas in 2009, a large portion these forest areas were also in LC scores of < 4, which resulted from harvesting practices prior to 1960, wildfires, clearance for agriculture and native forest conversion to plantation.

In areas beyond the mixed forest zone, the protection of mature forest at the suggested target of 20 % should still be applied. The protection of forest with mature trees in warmer habitats is important for the development of *Olearia argophylla* dominated mature forest and the protection other non-rainforest species that are sensitive to harvesting.

When evaluating which forests to harvest and which to protect, protection measures should be applied to sites that are naturally protected from wind and wildfire (refugia) and which are likely in the medium to long term to continue to provide habitat for rainforest species and mature eucalypts. The existing stream-side reserves will contribute to fulfilling this objective, providing areas with additional moisture which will assist in the protection of these forests even if the climate warms.

7.10.2 Mitigation measures for harvesting mixed forest and other mature forest areas

Ideally harvesting will avoid mature forest vegetation, particularly forest in which rainforest understoreys are well developed, since the results of this study have demonstrated that increased disturbance frequency reduces the opportunity for rainforest species to recover. However, where industry dictates that such forest will be harvested, consideration should be given to using specialized silvicultural methods such as smaller, disaggregated coupes, and/or variable retention silvicultural systems (Baker and Read 2011). Areas of the understorey dominated by rainforest trees and which are located within areas that could be naturally protected from mechanical damage from the combined effects of both harvesting and the regeneration burn, should be prioritised for retention. The harvest area should be minimised (~ < 10 ha) and designed so that the majority of the cut area is within 150 m of the mature forest edge within areas with a rainfall of more than 250 mm rainfall in the warmest quarter, and closer in areas where rainfall is less than this. Observational evidence in surveys for this thesis, which was borne out by evidence from other studies, suggests that the retention of logs and some trees (live or dead) will enhance the diversity and recovery rate in harvest areas. Logs and trees provide perches for birds, which encourages their visitation and delivery of bird dispersed propagules. Logs serves as nursery sites for establishment of many rainforest tree species, out of reach of browsers.

The development of techniques that result in cooler regeneration burns is also recommended as it is clear from the results of this thesis that many species would recover more frequently by vegetative reproduction if the burn intensity was reduced. Possible methods might include undertaking fires later in the season after soils and fuels have begun to increase in their moisture levels. Where fuels will not provide an

undue risk of wildfire, consideration could be given to top-burning (heaping the canopy branches and leaf material and burning this in smaller areas) and not undertaking a full high intensity regeneration burn. By reducing burn intensity, mature rainforest trees are more likely to survive the fire and resprout.

7.10.3 Mitigation measures in other wet forest types

Where the target forest for timber harvesting is not mixed forest, minimising distance to mature forest need not be prioritised. However, the recovery of some pioneer species, such as bradyspores, still depends on the local seed sources following harvesting. In most cases adjacent forest should contain the species targeted for harvesting. It may be possible to ensure that the harvest boundary is planned so that populations of uncommon species are omitted from the harvest area, or that at least some of the population is preserved in adjacent areas which can serve increase the opportunity for recolonizing the patch following fire.

7.10.4 Rotation periods

In much of the literature advocating the use of clearfell burn and sow for wet eucalypt forests, the policy of applying it at a rotation of 80 to 90 years has been advocated. Results from this thesis demonstrate that 80 to 90 years following a single wildfire is sufficient to return assemblages to something approaching old growth mixed forest. However, recovery rates may be slower in silvicultural forest. Targeting longer rotation times for some sites will assist in maintaining mature forest in the landscape.

Since the development of milling techniques to extract veneer from 40 to 50 year old trees harvesting has begun to occur in forests logged in the 1960s. Results of this thesis demonstrate that there is a considerable reduction in the reestablishment rates of mature forest species at sites disturbed at intervals of less than fifty years. This suggests that rotations of 50 years or less are likely to prevent the re-establishment of rainforest species.

It is advised that, in developing harvest plans for silvicultural regrowth forests less than 60 years in age, the distribution of rainforest regeneration be considered. Coupe boundaries should be developed so as to omit areas where rainforest saplings are well

established, and concentrate harvesting efforts in areas which are not as advanced in their development towards mixed forest.

7.10.5 Restoration

In areas where mature forest patches have become rare, passive or active landscape restoration may be worthwhile. In areas where harvesting has resulted in the removal of mixed forest from local areas, some areas should be selected for protection from future harvesting and prioritised for wildfire suppression, in order to ensure they have a greater opportunity for the eucalypts to reach maturity.

Within larger harvest sites, more rapid recovery of rainforest species could be achieved by assisting in the establishment of rainforest species in areas more remote from the mature forest edge. Local Environmental Non-Government Organisations have recently participated in the restoration of clear-fell burn and sow areas that were added to the Tasmanian World Heritage Area as part of the extension of the nomination to include a greater area of wet eucalypt forest. They achieved their restoration work by digging up seedlings of rainforest species that had naturally colonized the edge of the coupe in the first six month after the regeneration burn, and transferring them into areas of the coupe which were isolated from the edge (Tim Rudman personal communication 2/06/2015). Follow-up on the success (or otherwise) of this approach would indicate whether it may be viable for use in State forest areas where such targeted restoration would enhance landscape conservation. The advantages of this approach, provided hygiene measures are taken to prevent disease and weed spread, is that local provenance plants are used, and no seed collection is required. Measures to enhance likely success of the seedlings, such as the placement of protective branch-wood over seedlings to protect the plant from browsing or a rock nearby to assist with moisture retention could also be trialled.

7.11 Conclusion

This thesis demonstrated that LC does influence the diversity of vascular plants present within wet eucalypt forest patches in southern Tasmania. Parallel studies of beetles and birds have also demonstrated that these results are not restricted to plants alone. The rate of succession to mixed forest was found to be impacted by LC, but

other environmental constraints, especially disturbance history and climate also limit the opportunity for such successional processes to occur. Many common plant species were sensitive to LC influence, but the results showed that it was the species more common in mixed forest that were affected directly by LC. The pioneer species appeared to be affected indirectly by LC thought processes of competitive exclusion by rainforest species over time. The demonstration that LC may be as important as other environmental determinants of many plant species distributions, even within an intact forest region such as the present study area, has implications for forest management both here and elsewhere. Maintaining mature forest in the landscape is important for sustainable biodiversity management. Total area of mature forest habitat in surrounding landscapes measured at scales of 1 km radius and proximity to mature forest within silvicultural coupes are important metrics for assessing landscape resilience and recovery potential for harvest areas.

Mixed forest vegetation is a vegetation type which can be usefully viewed within the model framework of alternative stable states. It is likely to have a spatially stable distribution, which is distinct from both rainforest and wet sclerophyll forest. Within areas where natural fire regimes occur, the distribution of mixed forest is likely to be spatially determined by the interaction between climate and fire regimes but many environmental feedbacks including LC will ensure the stability of boundaries. Because mixed forest is reliant on a disturbance frequency sufficient to support eucalypt species, it is temporally less stable than rainforest or wet sclerophyll forest due to the extended time required before the rainforest trees achieve dominance in the understorey after disturbance. Changes to disturbance regime imposed by timber harvesting, and climate change may lead to the contraction of this vegetation.

Chapter 8 References

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Floristic response to landscape context in vascular plant communities in *Eucalyptus obliqua* and *Eucalyptus regnans* wet forest, southern Tasmania

Part B

APPENDICES

by

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Chapter 1 Appendix 1

1.1 Eucalyptus regnans: *a rainforest plant or a wet forest pioneer?*

Tng et al. (2012) put the case that *Eucalyptus regnans* may be better classified as a fire-adapted rainforest pioneer. However, traditionally this species has been placed along with other members of the genus *Eucalyptus sensu lato* as a member of the Australian autochthonous flora and is not usually treated as a rainforest species. Rainforest vegetation is generally accepted as comprising associations of species that due to their relative shade-tolerance are able to regenerate in the absence of catastrophic disturbance (Lynch and Nelder 2000). Certainly rainforest communities, even when at equilibrium with their environment, include many species that are only able to regenerate within the relatively well lit micro-habitats created by endogenous disturbance such as tree fall gaps and even lightning strikes, referred to as microseres (Hopkins 1981; Lynch and Nelder 2000). Compared with the other species occurring with *E. regnans* in wet eucalypt forests, saplings and older individuals of *E. regnans* had among the highest light compensation points (>300 lux, Ashton and Turner 1979). Species defined as rainforest trees (including *Nothofagus cunninghamii* and *Atherosperma moschatum*) had the lowest light compensation points (108 to 121 lux) and the small mesophyllous pioneer trees (including *Acacia dealbata, Bedfordia salicina, Cassinia aculeata, Pomaderris aspera* and *Prostanthera lasianthos*) all had intermediate light compensation points (Ashton and Turner 1979).

Tng et al. (2012) suggest that the gap created by catastrophic wildfire, which is necessary for the regeneration of *Eucalyptus regnans*, might be considered equivalent to the microseres in which many rainforest species regenerate. However, this extrapolation suggested in order to place *E. regnans* as a rainforest pioneer makes little sense unless other closely related and ecologically similarly wet forest species including *E. delegatensis* and *E. obliqua* (which also reach giant heights and dominate mixed forest) as well as the understorey species that regenerate in the same events, are also included. The main reason Tng et al. (2012) advocate separate treatment for *E. regnans* from the other eucalypts is its greater sensitivity to fire despite thickened

bark around the basal buttress and its general failure to resprout despite the presence of epicormic buds (Waters et al. 2010). Yet, rainforest species although often highly fire sensitive, are not typically defined on the basis of their lack of adaptation to fire; and are often able to resprout following at least mild fires provided the intervals between events are long enough (Barker 1991). Furthermore, despite the relative sensitivity if *E. regnans* to fire compared with *E. obliqua*, *E. regnans* often survives it (Ashton 1981a; Turner et al. 2009). A reason for excluding *E. obliqua* and other eucalypts as candidates for classification as rainforest pioneers is their greater environmental plasticity, occupying wide environmental ranges including dry forest and heathland vegetation, undermining their qualifications as rainforest species. Yet ecologically, although occupying a much narrower niche, *E. regnans* is performing the same ecological function within mixed forest as these other more widespread species.

The mixed forests, of which only some stands are dominated by *Eucalyptus regnans*, are functionally more like rainforest and share more species in common with rainforest than other wet eucalypt forests (Lynch and Nelder 2000). On this basis it could be argued that they should be classified as rainforests rather than as part of the wet eucalypt forest continuum (Lynch and Nelder 2000). The socio-political motivation for reclassifying mixed forests include the probability that they would be afforded greater levels of protection (Lynch and Nelder 2000). The treatment of mixed forest and rainforests would not necessitate the treatment of the component eucalypts as rainforest species.

Chapter 2 Appendices

2.1 Fire history of the study area

2.1.1 Pre European disturbance history

Fire has been a regular feature of many parts of Tasmania including the Southern Forests since the arrival of Aborigines during the last glacial period (ca 37,000 years BP, Cosgrove et al. 1990). Forests in the study area were then restricted to lowland river valleys (Kirkpatrick and Fowler 1998) where Aborigines sheltered in inland cave systems (Cosgrove et al. 1990; Loy et al. 1990). Following deglaciation and forest expansion, Aborigines adopted a coastal economy. The Huon Estuary, on the eastern edge of the study area, formed part of aboriginal territory (Ryan 2012). Despite a long history of aboriginal burning, both fire sensitive and disturbance dependent tree species were common in Holocene wet forests (Macphail 1979). Huge eucalypts were widespread over rainforest in the Southern Forest at the time of European invasion (Jackson 1968; Podger et al. 1988)

2.1.2 Post European disturbance history

Table 2-A. List of fires occurring in and adjacent to study area

Fire year, and mapped area	Areas reported to have burnt	Information source
1670	Silvicultural Systems Trial site, Warra LTER.	*Ring count by Alcorn et al. 2001.*
1740	Silvicultural Systems Trial site, Warra LTER.	*Ring count by Alcorn et al. 2001.*
1790	Silvicultural Systems Trial site, Warra LTER.	*Ring count by Alcorn et al. 2001.*
1851	6/2/1851: extensive areas burnt through the Huon district including She-oak hills at Judbury, Research Bay and Castle Forbes Bay.	*Huon Times* p 5, c 1.
1854	Extensive areas around Franklin, Huonville and Port Esperance.	The Courier, 13 Jan 1854 p 2; also Jan 14, 16 and 19th 1854.
1873	Silvicultural Systems Trial site, Warra LTER	*Ring count by Alcorn et al. 2001.*
1878	Castle Forbes Bay and Hospital Bay areas including Smith's, Hill's and Hawkin's tramway areas.	*The Mercury:* 5 Feb 1878, p 2, c 6.
1881	Surges Bay, Dover Valley including Andrewarthur's tramway area.	*The Mercury*, 25 Jan 1881, p3, c3.

Fire year, and mapped area	Areas reported to have burnt	Information source
1886	Geeveston and west of Kermandie including Hills, Geeves and Judd's tramway areas.	*The Mercury*, 8 Jan 1886, p 3, c6; 9 Jan 1886, p1, c9.
1898, >>6300 ha	Geeveston, Franklin, Castle Forbes Bay, and Port Esperance including the Speedwell sawmill tramway area, Hopkins Bros mill, Bennetts, Regan and Thompson's and Innes' Hoptoun saw mills.	*The Mercury*: 11 Feb 1898, p 3, c 2; 14 Feb 1898; 18 Feb 1898, p 4, c 2. *Regeneration Ages* Map
1903, 22 ha	Kermandie Divide area, Strathblane and Raminea including the tramways.	*The Mercury,11 Feb 1903, p7, c 5.* *Regeneration Ages* Map
1906, 2264 ha	Pear Hill/Huon River, Scotts Divide, Strathblane and Port Esperance areas including Strathblane tramways and mill, Chesterman's tramlines and Hopetoun mills.	*The Mercury,* 31 Jan 1906, p 4, c 7; 3 Feb 1906, p 6, c 1; 2 Feb 1906, p 6, c 1. *Regeneration Ages* Map
1912	Hopetoun sawmill area.	*The Mercury, 16 Feb 1913, p 3, c 6.*
1914, 4878 ha	Huon River-Warra Creek, Judds Creek/Judbury, Denison Hill, Bracken Ridge-Scotts Divide, New Rd, Geeveston area and Taylors Ridge-Kermandie Divide areas.	*The Mercury,* 11 Mar 1914, p 4, c 8; 27 Oct 1914, p 3, c 4. *Regeneration Ages* Map
1918	Warra Long Term Ecological Research (LTER) Site.	*Ring count by Hickey et al. 1999*
1920, 154 ha	Kermandie Divide area.	*The Mercury,* 12 Jan. 1920, p 4, c 7; 18 Feb. 1920, p 4. c 7. *Regeneration Ages* Map
1922, 1778 ha	Russell River and Judds Creek areas.	*Regeneration Ages* Map
1934, 16465 ha	Arve River Valley, Judbury, Geeveston and Denison River Valley areas including areas around Mr Beachs', Mr Bennetts' and Mr Ashlin's mills.	*The Mercury*, 17 Jan, 1934, p 8, c 4; 19 Jan 1934, p 11, c 1. *Regeneration Ages* Map
1939	The Russell River Forestry Camp area. (Bushfires in Southern Tasmania burnt 11,440 acres of land, half of which were commercial forest.)	*The Mercury*, 1 Feb, 1939, p 7, c 5; and 15 Feb 1939, p 7, c 2; Dept Forestry Annual report 1938/39, Tasmanian Government, Hobart.
1939/40 20 ha	Weld plains confluence of the Weld and Huon Rivers 29/12/1939.	*Edgley (1960) Forestry Tasmania unpublished report*
1941/42	Arve River Valley area including Bennetts tramway.	*The Mercury, 27 Dec 1941, p 2, c 7; 29 Dec 1941, p 5, c 4.*
1944	Warra LTER Site	*Ring count by Hickey et al. 1999*
1945/46	Lonnavale, Denison River Valley, both sides of the Russell River and Upper Russell River Valley and areas behind Judbury. Southern Tasmania 1150 acres of merchantable forest burnt, 1840 acres of seedlings and saplings, 1703 acres of scrub was burnt on State forest land; another 4500 acres of crown	*The Mercury,* 28 Dec 1945, p 2, c 5; 31 Dec 1945, p 1, c 1; 5 Jan 1946, p 20, c6. Dept Forestry Annual report 1945/46, Tasmanian Government, Hobart.

Fire year, and mapped area	Areas reported to have burnt	Information source
	land was also burnt.	
1946/47	South Creek including Hermon's tramway and mill area.	*The Mercury*, 26 Dec 1946, p 6, c 5.
1947/48	Picton River valley area. (40,288 acres of state forest burnt in southern district, most of it was scrub, 100 acres of merchantable timber, 410 acres of regrowth, 210 acres of cutover forest.)	*The Mercury*, 4 Feb 1948, p 2, c 1; and 9 Feb 1948, p 6, c 5. Dept Forestry Annual report 1947/48, Tasmanian Government, Hobart.
1950/51	Franklin, Judbury and Geeveston, Waterloo, Raminea, Kermandie, Lonnavale, Arve Valley, Huon River, Weld River and Glen Huon areas including Hermon's mill and tramway area at Riley Creek, Hill's property on Scotts Road, and Batchelor's and Helm's mill areas.	*The Mercury*, 8 Sep 1950, p 1, c 4; 5 Dec 1950, p 1, c 4; 6 Feb 1951; 12 Feb 1951, p1, c1; 22 Feb 1951.
1955	Warra LTER Site	*Ring count by Hickey et al. 1999*
1961, 938 ha	Denison and Little Denison River Valley area.	*Regeneration Ages* Map
1963, 219 ha	Kermandie Divide area.	*Regeneration Ages* Map
1966/67, 4,690 ha	Arve River Valley, Blue Hill, Scotts Divide and Judbury.	*Regeneration Ages* Map
1975, 37 ha	McDougalls Rd area above Russell River.	*Regeneration Ages* Map
1981, 277 ha	Hartz mountain area.	*P&WS Fire database*
1983, 56 ha	Hartz mountain area.	*P&WS Fire database*
1987, 2 ha	Hartz mountain area.	*P&WS Fire database*
1991, 2 ha	Scotts Divide area.	*Regeneration Ages Map*
2000, 11 ha	Cooks Creek Area, west Picton area.	*PI Map 2009*
2002, 15 ha	Blakes Opening.	*P&WS Fire database*
2003, 10 ha	Blakes Opening.	*P&WS Fire database*

Abbreviations: P&WS = Tasmanian Parks and Wildlife Service

2.2 Vegetation classification for study area

Table 2-B. Disturbance-based rule-set for vegetation classification

Code ^	Code elements present	Code elements absent	Notes describing exceptions and additions
AGRIC	V	E, ER, M, P.	Exclude: V & E→SILVP; V & ER1→SILYR V & ER2-6→SILOR
PLNTN	P	E, ER, M,V.	
RAINF	M	E, ER, P.	See NOFOR and OTHNF for additions
MIXED	E/ER with M / MR		Add: areas mapped with over mature eucalypt (om) without ER for which there is no wildfire or logging record
NOFOR	S/W/K	E, ER, M, T, P.	Exclude: areas where NOFOR intercepts TASVEG rainforest →RAINF
OTHNF	T	E, ER, M, P.	Exclude: areas where OTHNF intercepts TASVEG rainforest →RAINF
WFMAT	E	M, V, P.	Exclude: areas with >5% E mapped in 1950 as AGRIC→ SILVP
WFRGY	ER (< 50 yrs) Unaged ER1–3	E, M, Mr, P.	Exclude: areas of ER if subject to previous clearance for agriculture or logging in past ~50 yrs: ER1/ ERg→ SILYR ER2/ER3/ERp→SILOR
WFRGO	ER (> 50 yrs) Unaged ER4–6	E, M, Mr, P.	
SILYR	ER (< 20 yrs) Unaged ER1 OR ER1 & V	E, M, Mr, P.	Include unaged regrowth as SILYR only if it is in an accessible area (all years) for which no mapped wildfire after 1947 accounts for presence of young eucalypt regrowth. Include any ER logged or cleared more than 50 years ago but burnt in wildfires in most recent 19 year period.
SILOR	ER (30–50 yrs) OR Unaged ER 2–3 OR ER2-6 & V	E, M, Mr, P.	Include unaged regrowth as SILYR only if in an accessible area (all years) for which no mapped wildfire after 1947 accounts for presence of regrowth (of reduced size since 1947). Add: ER logged or cleared more than 50 years ago but burnt in wildfires between 20 to 50 years ago.
SILVP	E with V OR E with ER aged < 50 yrs OR Unaged ER1–2	M, P.	Include unaged regrowth as SILVP only if an accessible area (all years) and no mapped wildfire after 1947 accounts for presence of regrowth; Include any E logged more than 50 years ago & disturbed by wildfire in past 50 years Exclude E logged more than 50 years ago & not mapped as AGRIC in 1950→WFMAT

Abbreviations and definitions for code elements used in Table 2–B:

^ Code for vegetation class code definitions (see Part A: Table 2–1)

→ reallocate to alternative class

E = mature eucalypts with crown density classes > 5%;

ER = regrowth eucalypts with crown density > 5%;
Height classes: **ER1** < 15 m, **ER2** 15–27 m, **ER3** 27–37 m, **ER4** 37–44m, **ER5** 44–50 m, **ER6** > 50 m;

K = bracken fernland;

M = myrtle (*Nothofagus cunninghamii*) rainforest;

P = plantation;

S = small trees and shrubs with a height potential of less than15 m;

T = secondary tree species taller than 15 m;

V = agriculture;

W = native vegetation in which trees are uncommon.

2.2.1 Description of PI codes and their interpretation for vegetation classification

Photographic interpretation of aerial imagery is used to assign areas of similar vegetation a PI code, which consists of a string of structural vegetation elements in order of commercial importance. If present, mature eucalypts with a density greater than 5% are listed first, while regrowth eucalypts with a crown density of more than 5% are listed next. Where the regeneration year is known it is reported in the PI code. For unaged eucalypt regrowth, the height and density are indicated in the PI code. Other condition data indicating disturbance is also provided in the code, including fire-damaged (fd) and cut-over (co).

2.2.2 Description of Vegetation Classification

In the first step of classification PI mapping polygons were allocated a class on the basis of vegetation structural elements recorded in the PI code (Table 2–B). This allocated all eucalypt forest of known age to silvicultural classes, and all unaged eucalypt forest to wildfire classes, irrespective of disturbance data.

The second classification step involved the reassignment of polygons on the basis of disturbance data. All vegetation which had ever been recorded as logged or cleared previously was allocated to a silvicultural class if disturbed in the most recent 50 year

period even if wildfire was the most recent disturbance (Table 2–B). Where aged regeneration was associated with a wildfire event and no previous logging history was recorded polygons were reassigned to the most appropriate wildfire vegetation classes (WFMAT, WFRGY, WRFGO).

Finally patches mapped as NOFOR or OTHNF (Table 2–B) were reassigned to RAINF where their distribution coincided with areas mapped as rainforest in *TASVEG* 2.0.

2.2.3 Assumptions made classifying vegetation using PI maps

The 1947 mapping did not record the regeneration year and regrowth eucalypts were classified as sapling, pole and spar rather than by height classes. I assume on the basis of data provided by Ashton (1975) that eucalypts become poles at about 15 years when they are over 15 m tall, and spars at 40 years when they are over 45 m tall. I assume the sapling class (ERg) is directly equivalent with ER1 (< 15 m); poles (ERp) span height classes ER2 (15–27 m), ER3 (27–37 m) and ER4 (37–44 m); and spars (ER) span classes ER5 (44–50 m) and ER6 (> 50 m).

The PI mapping for 1985 and 2009 recorded the mechanism of regeneration, but only for sapling age regrowth (< 15 m tall) of known regeneration age. For areas not provided with this information in PI mapping or 'Regeneration ages' map I assume that ER1 and ERg regrowth height classes occur in areas regenerated in the last 19 years, while ER2, ER3 and ERp correspond to 20–50 year old trees. Fire damaged and cut-over data were assumed to indicate a wildfire or harvesting operation within the decade prior to the year of mapping.

All areas with unaged eucalypt regrowth (>5% cover) on the 1947 PI map were assumed to have been burnt in wildfires in the preceding 50 years. Those regrowth areas within 500 m of an access route, mill or road were also assumed to have been logged if their height provided an estimated age corresponding with the operating dates of the tramway, road or mill. In 1985 and 2009 unaged eucalypt regrowth areas were only assumed to have been logged since 1947 if tree heights were shorter than previously mapped, not within a known wildfire area corresponding with their estimated age and within 500 m of an access route or mill operating at a time which corresponded with the estimated regrowth age.

2.3 Spatial data sources

Table 2-C. Sources of spatial information used in analyses

Information	Map layer	Author	Method of mapping	Meta-data notes
1000 mm isohyet	*BIOCLIM* (climatic rasters).	Landscape Logic (2008).	Busby 1991.	100 m resolution.
600 m contour	2nd edition 25 metre Digital Elevation Model.	Information & Land Services 2002.	Arcinfo TIN modelling of 10 m contours.	25 m resolution.
Vegetation 1947; Vegetation 1985; Vegetation 2009	*Forest-type maps* (PI maps): 1947, 1985, 2009.	Forestry Tasmania unpublished maps: 1947, 1985, 2009.	Stone (1998), see also Appendix C.	See Appendix 2.3 for metadata.
Rainforest 2009	*TASVEG 2.0*.	Tasmanian Vegetation Monitoring & Mapping Program 2009.	Harris and Kitchener (2005).	1:25,000 mapping scale from 1:42000 colour aerial photography: 1996/2000/2001.
Disturbance year/type (clear-felling, wildfire):1897-2009	*Regeneration Ages* map; PI maps: 1947, 1985, 2009; *Fire history* map.	Forestry Tasmania unpublished and undated map; Forestry Tasmania unpublished maps: 1947, 1985, 2009; Tasmanian Parks & Wildfire Service, unpublished: sourced 2011.	Hickey et al. (1999).	*Regeneration Ages* map provides partial temporal and spatial coverage of the study area (1898 to 1992).
Tramways, mills and roads: 1897-2009	PI map 1947; Tramways/mills; *Forestry Roads* layer.	Forestry Tasmania Unpublished maps: 1947; Figure 4 in Kostoglou 1995; Forestry Tasmania Unpublished map: sourced 2010.	*Tramways & Mills*: Kostoglou (1995).	Mill & tramway operating years: Kostoglou 1995; Road construction years: Forestry Tasmania Annual reports. All mapping 1:25,000–1:36,680.

2.4 Meta data for PI maps

Table 2-D. Meta data for PI maps

Landscape year	Mapping scale	Details of Photography	Notes
1947	1:36,680	Black & white, 1:15,840 1947	Original paper copies of forest-type PI maps were scanned, ortho-rectified and digitised by Liam Hindrum and Jayne Balmer (2010), Forestry Tasmania files. A few areas not mapped due to incomplete photographic coverage were filled on the basis subsequent mapping data and disturbance history for these areas. Horizontal accuracy of the mapping was poor (±100 m) and the detail of the mapping was variable but generally comparable to later mapping. The median size of mature forest patches was 4 ha and 36% of both mature forest patches and silvicultural patches were under 2 ha.
1985	1:25,000	Colour 1:20,000 1980, and 1984	The oldest archived digital PI map for the area included some polygons inserted into the mapping for area logged or converted to plantation between 1986 and 1996. The mapping classes for these polygons were deduced for the 1985 year from information retained in slivers surrounding the inserted polygons and other mapping sources. The horizontal accuracy of the mapping is good (±25 m). The detail of mapping varies between forest types. More than half silvicultural regrowth polygons are under 2 ha. Mature forest polygons under 2 ha are rare and the median size is 12 ha, and mode 9 ha.
2009	1:25,000	Colour 1:20,000, 2002	Since PI mapping based on the 2002 aerial photography, Forestry Tasmania has annually updated the digital mapping by inserting polygons corresponding to areas known to have been logging or converted to plantation during the previous year using ground survey data. A copy of the mapping is archived at the end of each financial year. The horizontal accuracy of the mapping is good (±17 m). 10% of mature forest polygons are under 2 ha, while the median size is10 ha and mode 7 ha.

2.5 Distribution of vegetation classes in study area by year

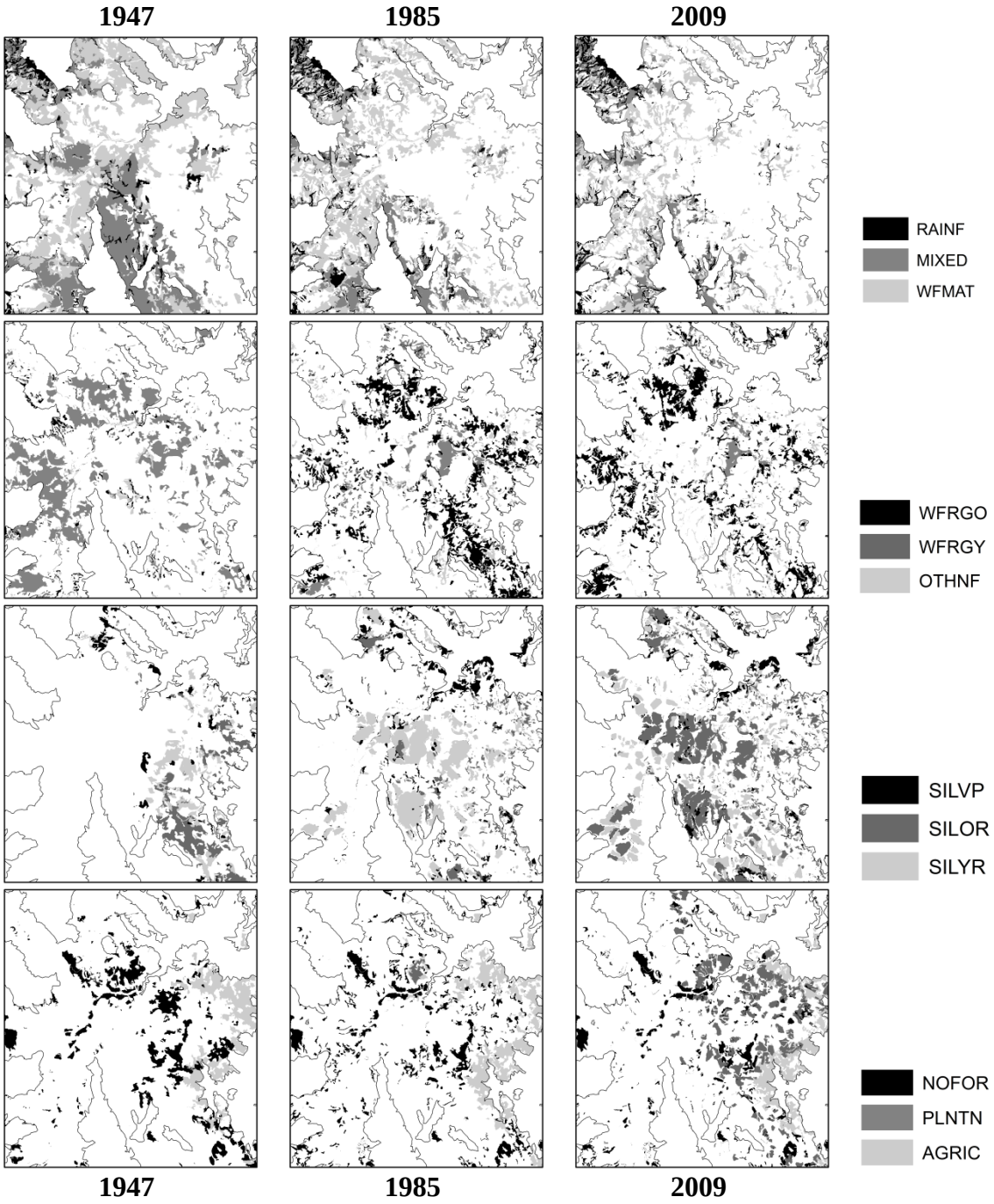


Figure 2-A. Distribution of twelve vegetation classes by year within study area

See Part A: Table 2–1 for definition of vegetation codes.

2.6 Areas disturbed between 1947 and 2009

Table 2-E. Estimates of extent of disturbances within study area between ~ 1897 and 2009.

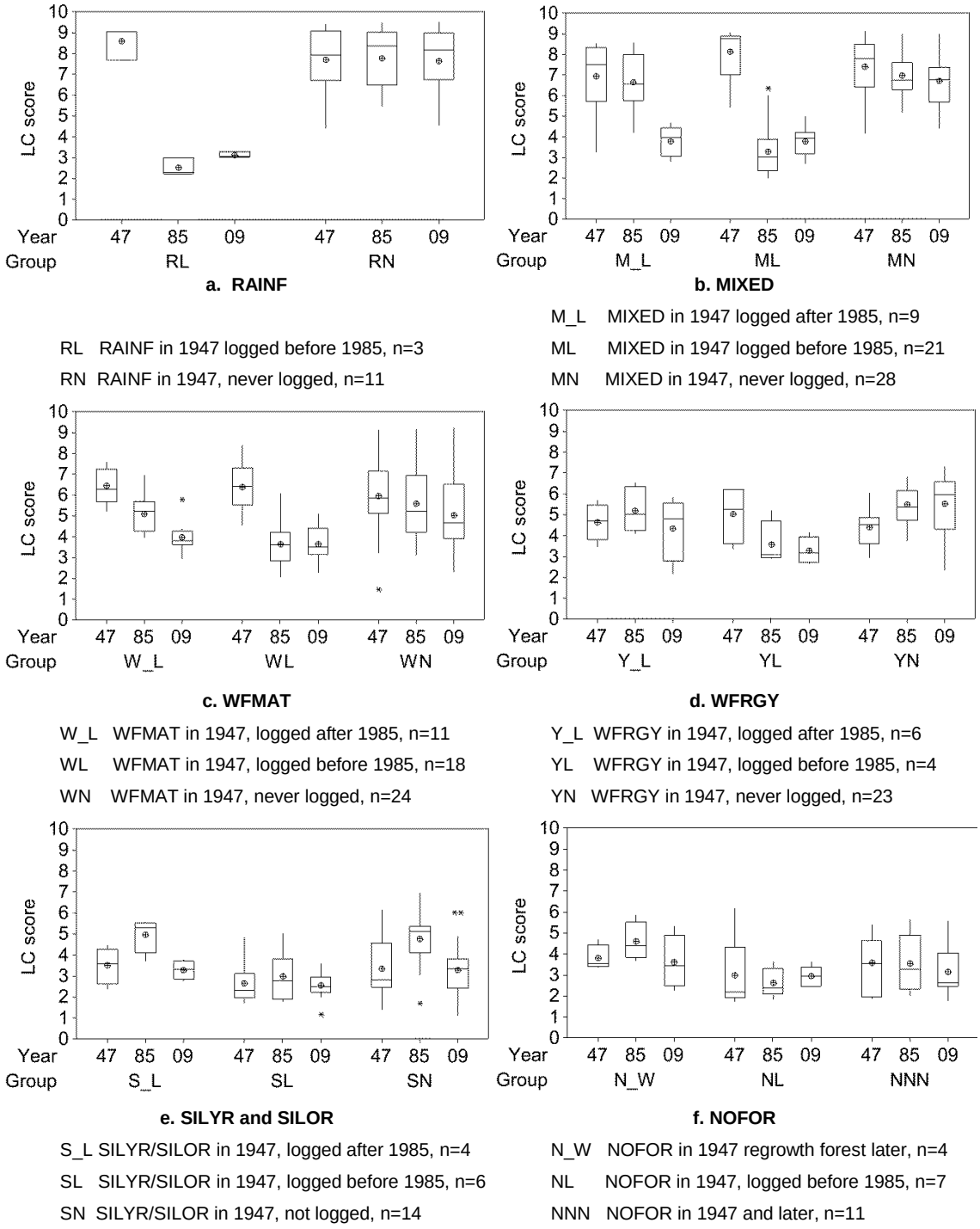
	~50 years prior to 1947	**1947 to 1985**	**1985 to 2009**	**2009 area**	**~1897 to 2009**
Wildfires					41,100 ha (56%)
Fires: mapped & deduced	37,413 ha (51.5%)	7,415 ha (10.2%)	360 ha (0.5%)	~23,150 ha forest (31.9% of study area) in 2009 burnt in wildfires but not logged/ cleared	
Harvested					24,850 (34.3%)
Logging*	9,100 ha (12.6%)	11,450 ha (15.7%)	7,650 ha (10.5%)	~20,650 ha of forest in study area in 2009 have been harvested	
Clearance				1300 ha forest old fields	12,100 ha (16.7%)
Native vegetation cleared for Agriculture	4,500 ha (6.1%)	2,450 ha (3.4%)	500 ha (0.7%)	4250 ha	
Native vegetation cleared for Plantation	0	300 ha (0.4)	4,350 (6.0%)	6300 ha	
Agricultural land converted to Plantation	0	7 ha (0%)	1,680 (2.3%)		
No disturbance mapped					12,500 ha (17.2%)
Mature forest types (RAINF, MIXED, WFMAT)				~10,150 ha (14.0%)	
Other forest (OTHNF)				2,350 (3.2%)	
Non-forest vegetation (NOFOR)				4450 (6.1%)	2,150 ha (2.9%)
Study area				72,600 (100%)	

*Excludes areas logged prior to clearance and forests only subject to thinning operations

2.7 Landscape context of each vegetation class

Table 2-F. Mean LC scores by landscape radius and year for each vegetation class

LC score mean ± std dev									
Landscape:	**500 m radius**			**1 km radius**			**2 km radius**		
Year:	**1947**	**1985**	**2009**	**1947**	**1985**	**2009**	**1947**	**1985**	**2009**
RAINF	7.8 ±1.5	7.8 ±1.4	7.5 ±1.6	7.4 ±1.5	7.3 ±1.5	7.0 ±1.6	7.1 ±1.5	6.9 ±1.4	6.7 ±1.5
MIXED	8.1 ±1.1	7.3 ±1.3	7.3 ±1.3	7.7 ±1.2	6.8 ±1.3	6.7 ±1.4	7.3 ±1.1	6.4 ±1.2	6.2 ±1.3
WFMAT	6.4 ±1.1	6.1 ±1.2	5.9 ±1.4	6.2 ±1.2	5.8 ±1.3	5.6 ±1.5	5.9 ±1.3	5.5 ±1.3	5.3 ±1.4
WFRGO	5.9 ±1.6	5.3 ±1.2	5.2 ±1.4	6.0 ±1.7	5.0 ±1.2	4.9 ±1.4	6.1 ±1.6	4.8 ±1.2	5.9 ±1.6
WFRGY	4.7 ±1.4	4.4 ±1.1	4.5 ±1.3	4.1 ±1.2	4.5 ±1.2	4.4 ±1.3	3.9 ±1.2	4.7 ±1.3	4.4 ±1.3
OTHNF	3.6 ±1.1	6.0 ±1.5	5.1 ±1.7	4.6 ±1.7	6.3 ±1.6	5.0 ±1.8	4.4 ±1.8	6.4 ±1.5	5.0 ±1.8
SILVP	4.5 ±1.4	4.3 ±1.2	3.9 ±1.1	4.7 ±1.5	4.3 ±1.3	3.7 ±1.2	5.0 ±1.5	4.2 ±1.3	3.6 ±1.2
SILOR	3.2 ±1.2	3.4 ±1.2	3.4 ±1.0	3.4 ±1.3	3.6 ±1.3	3.5 ±1.1	3.5 ±1.4	3.7 ±1.3	3.7 ±1.1
SILYR	2.7 ±1.2	3.0 ±1.1	3.4 ±1.0	3.0 ±1.3	3.5 ±1.2	4.0 ±1.1	3.3 ±1.3	3.9 ±1.2	4.3 ±1.1
NOFOR	2.8 ±1.4	3.8 ±1.5	3.3 ±1.5	3.4 ±1.6	4.3 ±1.4	3.7 ±1.4	3.9 ±1.5	4.6 ±1.2	4.0 ±1.4
PLNTN	-	1.7 ±0.8	1.9 ±0.9	-	2.2 ±0.6	2.4 ±0.9	-	3.5 ±0.3	2.8 ±0.8
AGRIC	1.4 ±0.9	1.7 ±0.9	1.5 ±0.8	1.8 ±1.0	2.0 ±0.9	1.7 ±0.8	2.1 ±1.0	2.3 ±0.8	1.8 ±0.7
Whole Area	5.3 ±2.4	4.8 ±2.1	4.3 ±2.1	5.3 ±2.2	4.8 ±1.8	4.3 ±1.8	5.3 ±2.0	4.7 ±1.6	4.3±1.7



RL RAINF in 1947 logged before 1985, n=3

RN RAINF in 1947, never logged, n=11

M_L MIXED in 1947 logged after 1985, n=9

ML MIXED in 1947 logged before 1985, n=21

MN MIXED in 1947, never logged, n=28

W_L WFMAT in 1947, logged after 1985, n=11

WL WFMAT in 1947, logged before 1985, n=18

WN WFMAT in 1947, never logged, n=24

Y_L WFRGY in 1947, logged after 1985, n=6

YL WFRGY in 1947, logged before 1985, n=4

YN WFRGY in 1947, never logged, n=23

S_L SILYR/SILOR in 1947, logged after 1985, n=4

SL SILYR/SILOR in 1947, logged before 1985, n=6

SN SILYR/SILOR in 1947, not logged, n=14

N_W NOFOR in 1947 regrowth forest later, n=4

NL NOFOR in 1947, logged before 1985, n=7

NNN NOFOR in 1947 and later, n=11

Figure 2-B. Interquartile range boxes and mean LC score (1 km radius) by year for random points grouped according to vegetation class in 1947 and whether that location point was not logged after 1947, logged before 1985 or logged after 1985.

Chapter 3 Appendices

3.1 Supplementary methods

Soil data for each plot were derived from a 10 cm core of surface soil, air dried within 48 hours and stored in a paper bag in a cool dry area. Prior to analysis each soil was sieved using a 2 mm sieve to remove leaf litter, roots and rocks and ground in a mortar and pestle. The soil pH and conductivity were measured using a Palintest pH meter and an Elmetron CPC-411 conductivity meter, calibrated on each day of testing. For pH a 1:4 solution of soil to distilled water was shaken for one minute prior to the reading. For conductivity a 1:5 solution of soil to distilled water was shaken for 2 minutes and allowed to settle before reading the conductivity (Palintest Ltd, soil testing kit instruction manual, undated). Nitrogen and carbon were analysed using a Perkins Elmer Series II 2400 CHNS/O Elemental Analyser following the manufacturer's protocol.

Temperature and relative humidity data were measured in plots along the middle transect every 30 minutes for a period of 142 days between December 2011 and May 2012 using HOBO U23 pro V2 temperature/humidity data loggers (ONSET, Massachusetts). The loggers were mounted 50 cm from the ground on a steel post with solar protection shields. Vapour pressure deficit (VPD) was calculated from temperature and humidity using the following formulas (Allen et al. 2005):

Saturation Vapour Pressure: SVP= 0.6108 exp[(17.27*temp)/(temp+237.3)]

Actual Vapour Pressure: AVP=(humidity/100) * SVP

Vapour Pressure Deficit: VPD = SVP - AVP

Monthly average climate variables were calculated for each of four complete months in 2012, January to April (Table 3–A). Extreme records due to equipment malfunction were removed before averages were calculated. This variable set was tested for correlation with species assemblage using Distlm and from among those most associated with assemblage four were selected for use as predictor variables: Mean afternoon VPD in February, Mean daily VPD in April, Mean daily minimum temperature for January and Mean daily temperature for April. The data calculated for

each plot along the middle transect were used also for the corresponding distance on the adjacent transects.

Table 3-A. Monthly Temperature (Temp) and Vapour Pressure Differential (VPD) variables calculated and tested for their association with floristic responses. Ticks show those selected as potential response predictors.

Code	Variable	Calculation method.	Temp	VPD
Pm	Afternoon average	Average of observations from 1300 hrs until 1600 hrs.	☐	☑ Feb
Sh	Average for ten sunshine hours	Average of all observations from 0800 hrs until 1800 hrs.	☐	☐
Dy	Daily average	Average of all observations from 0030 hrs until 2400 hrs	☑ April	☑ April
Ch	Daily average change rate	Daily average of change in observation from the previous 30 min recording.	☐	☐
Mn	Minimum daily	Minimum recorded for the day	☑ Jan	☐
Mx	Maximum daily	Maximum recorded for the day	☐	☐
Ra	Daily range	Daily difference between minimum and maximum observation	☐	☐

Interpolated climate data were extracted from the 2007 state-wide coverage for seven BIOCLIM parameters (Nix and Busby 1986) prepared by the Landscape Logic project using the ESOCLIM© module of ANUCLIM© Version 5.2 (Houlder et al. 2000) and a 25 m digital elevation model. The parameters selected were those found to be most closely associated with the wet eucalypt forest community variation in preliminary analyses of other data (chapter 4): annual mean temperature (TAM), temperature seasonality (TSE), maximum temperature (TMX), precipitation of the warmest quarter (PWM) and radiation of the lowest period (RLP).

Topographic variables were generated from the 25 m state-wide Digital Elevation Model and where appropriate using a 3 by 3 grid cell kernel: aspect, percentage slope, flow accumulation, profile curvature, plan curvature and average curvature. Topographic position index was calculated as the difference between the elevation of the cell and the mean elevation of all cells in a buffer radius of 200 m (Jenness 2006). Northness index (Holden et al. 2009) was calculated by multiplying the percentage slope by the cosine of the aspect (in degrees). This calculation was adjusted by adding 45 degrees to the aspect to calculate Northwestness, an indicator of exposure to the sun at the driest time of the day.

Fire frequency in the last 120 years was estimated for each plot using fire history maps and forest inventory maps (PI maps) for 1947, 1986 and 2010. Regrowth forest age was also derived from the 2010 forest inventory map.

The average environmental dissimilarity of the regrowth plot to the nearest two mature forest plots was calculated by first doing a Principal Components Analysis of the full data set (regrowth and mature forest plots) using data for the 14 variables most highly associate with species assemblage. The first three PCA axis scores were then used to produce a relative Euclidean distance matrix from which the dissimilarity of each plot with the nearest two mature forest plots were extracted and averaged. The relative cover of mature forest indicator species in the nearest mature forest plot was calculated as an average of the relative cover of these species within the understorey of the two mature forest plots for each transect (excluding eucalypt canopy cover); this variable was used for each silvicultural plot along the transect.

Model selections in gamlss were made on the basis of Bayesian Information Criterion (BIC). The iterative model development process began by fitting a null model to the response (y~1) and specifying different distribution families to determine the distribution of best fit for the response variable. Next the random effect structure was explored using BIC and residual diagnostic plots. The regression software Random Forests (Liaw and Wiener 2002) was used to screen the variables for those likely to best predict the response variable. A full model with the most likely predictors from among those with the least autocorrelation were assessed using the drop term function which automatically dropped each term and reported the chi-square probability that its deletion resulted in a loss of fit for the model. These methods provided an initial group of predictors which were used together with age and distance from the edge to commence building the best model formula for mu. Models were then built by starting with age and distance and adding and dropping terms. A predictor was retained in the model only if its addition caused a reduction in the BIC and there was evidence that the association with the response variable was greater than could be expected by chance variation with a alpha level of probability less than or equal to 0.05. Due to the small number of sites the only interactions tested between predictors was that of age and distance. A model for sigma was developed for beta-distributed response variables.

3.2 Supplementary Results

3.2.1 Floristic composition variation with DMFE

3.2.1.1 Assemblage variation

There were 108 vascular plant species recorded from the 15 sites. Only two rainforest species were not found in any of the silvicultural regrowth forest plots (*Crepidomanes venosum, Pseudopanax gunnii*). Only 66 of the species were found in mature forest plots. Five species of eucalypts were recorded, but only two of these were common (*E. obliqua* and *E. regnans*). Among the 103 understorey species, 32 were categorised as MFI species, 10 as other rainforest species, 17 as SFI species, and 44 as other pioneer species. Of the 101 understorey species occurring in regrowth plots there were 88 species found in near plots (15 and 35 m from the mature forest edge) and 87 species found in the far plots (120 and 200 m from the edge).

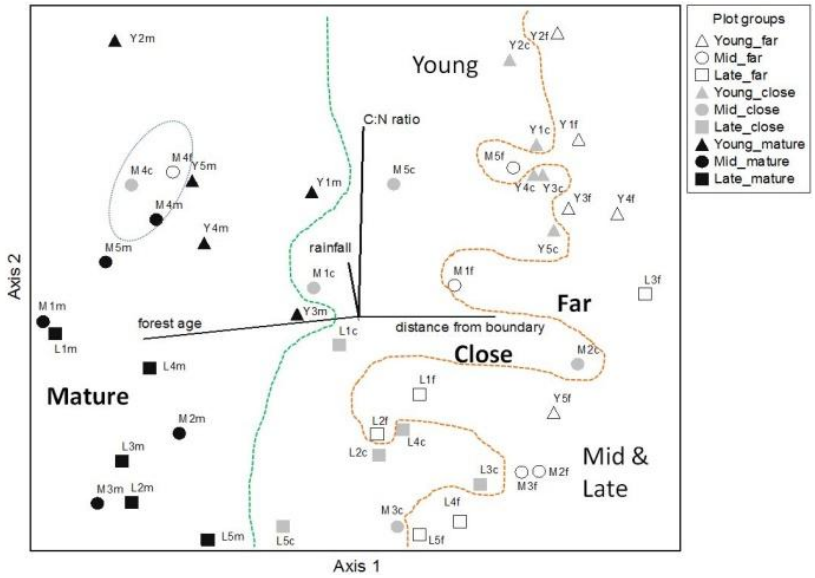


Figure 3-A. Non-metric multidimensional scaling ordination of average species cover data for three distance classes within each site (stress = 14.5%).

Note: Annotations are shown in Figure 3-A to distinguish the difference between regrowth and mature forest assemblages, and noticeable directionality in assemblage differences associated with regrowth age (young-stage sites with high axis 2 scores) and DMFE (far plots high axis 1 scores). An oval is drawn around the mid-stage site 4 plots to highlight their similarity with the adjacent mature forest.

Two axes were sufficient to describe the relationship among plots. The first axis of the NMS ordination was strongly associated with both DMFE (Pearson's R = 0.67) and forest age (R = -0.85) demonstrating the major floristic difference between mature and regrowth forests. An exception was the regrowth at the fourth mid-stage site, which was floristically indistinguishable from mature forest. The rainforest trees at this site were recovering from regeneration vegetatively, suggesting the regeneration burn had been particularly cool. All other regrowth plots were well separated from their associated mature forest along axis one although they were approximately aligned along the second axis. Far plots generally had higher axis one scores than the near plot of the same site although they were generally floristically similar and this data set had insufficient power to distinguish whether these plots were floristically distinct. The second axis was most strongly associated with the Carbon-Nitrogen ratio (Pearson's R 0.67), high scores representing sites with more carbon than nitrogen, which corresponded with regrowth sites regenerated most recently. Rainfall was also more weakly associated with axis 2 (R = -0.19) (Figure 3–A).

Twenty two variables were associated with regrowth forest assemblages (Distlm, $P < 0.01$, $R^2 = 63\%$). The highest ranking 15 each contributed more than 1% to accumulated R^2 and together accounted for 56%: age, ratio of soil carbon to nitrogen, radiation in the lowest week, temperature seasonality, April mean daily vapour pressure differential (VPD), soil pH, April mean daily temperature, northwestness, cosine of aspect, topographic index, mean annual maximum temperature, mean precipitation for the warmest quarter, January mean minimum daily temperature, mean February afternoon VPD and percentage slope. DMFE ranked last among the 22 site variables contributing to species assemblage.

DMFE was strongly associated with environmental dissimilarity to the closest mature forest (Rho = 0.61, $P < 0.00001$ Table 3-B). Other variables positively associated with DMFE included mean daily VPD, temperature in April and VPD in February. Regrowth age was associated at least weakly with all but four of the variables tested. The strongest correlations with age were January minimum temperature (positive), mean February afternoon VPD (negative) and soil carbon-nitrogen ratio (negative). The association observed between age and topographic variables provides further evidence of sampling biases among the site age-classes (Table 3–B, Figure 3–B).

3.2.1.2 Correlation among environmental predictors of forest assemblage

Table 3-B. Spearman's Correlation (*P*-Value #) for environmental dissimilarity to mature forest (ED), DMFE & 16 other predictors.

Rank^	variable	ED	22. DMFE	1. Age	2. C:N	7. pH	8. NWS	9. CAS	10. TIN	15. Slope
E.D.	ED	1	**0.61 (4)**	**-0.21 (1)**	**0.26 (3)**	0.04 (ns)	-0.09 (ns)	0.06 (ns)	0.05 (ns)	**0.25 (2)**
23	MFI species cover in mf plot*	-0.05 (ns)	0 (ns)	**0.26 (3)**	-0.00 (ns)	-0.02 (ns)	**0.21 (1)**	-0.01 (ns)	0.02 (ns)	**0.36 (4)**
22	Distance (m) to mature forest edge (DMFE)	**0.61 (4)**	1	0 (ns)	0.04 (ns)	0.03 (ns)	0.09 (ns)	0.05 (ns)	0.07 (ns)	-0.07 (ns)
1	Age (years)	**-0.21 (1)**	0 (ns)	1	-0.27 (3)	**0.15 (1)**	-0.16 (wk)	**0.14 (4)**	**0.27 (3)**	-0.02 (ns)
2	Carbon-Nitrogen ratio	**0.26 (3)**	0.04 (ns)	**-0.27 (3)**	1	**-0.28 (3)**	**-0.35 (4)**	**-0.28 (3)**	**-0.28 (3)**	0.02 (ns)
7	Soil pH	0.04 (ns)	0.03 (ns)	**0.15 (1)**	**-0.28 (3)**	1	0.1 (ns)	0.08 (ns)	0.08 (ns)	**0.23 (2)**
3	Radiation lowest week (RLP)	0.04 (ns)	0.01 (ns)	0.12 (sm)	**-0.28 (3)**	0.08 (ns)	**-0.29 (3)**	**0.19 (1)**	**0.45 (4)**	**-0.21 (1)**
4	Temp seasonality (TSE)	0.13 (sm)	-0.02 (ns)	0.07 (ns)	0.07 (ns)	-0.04 (ns)	**-0.24 (2)**	0.17 (ns)	0.09 (ns)	-0.15 (wk)
5	VPD April mean	**0.5 (4)**	**0.28 (3)**	**-0.25 (2)**	**0.19 (1)**	0.06 (ns)	-0.07 (ns)	0.09 (wk)	**-0.23 (2)**	**0.18 (1)**
6	Temp April mean (TApril)	**0.21 (1)**	**0.28 (3)**	-0.09 (ns)	-0.12 (sm)	-0.02 (ns)	0.39 (4)	0.16 (wk)	**-0.34 (4)**	0.14 (wk)
11	Annual Temp mean maximum (TMX)	**-0.18 (1)**	-0.06 (ns)	**0.17 (1)**	-0.14 (wk)	-0.13 (wk)	0.07 (ns)	0.07 (ns)	**-0.34 (4)**	-0.06 (ns)
12	Precipitation warmest quarter (PWM)	-0.01 (ns)	0.01 (ns)	-0.16 (wk)	**0.31 (4)**	0 (ns)	0.26 (2)	-0.22 (2)	**-0.35 (4)**	0.12 (sm)
13	Temp January mean daily minimum (MnTemp.J)	-0.16 (wk)	0.09 (ns)	**0.46 (4)**	**-0.36 (4)**	0.04 (ns)	0.29 (4)	0.16 (wk)	-0.11 (ns)	-0.02 (ns)
14	VPD pm February mean	**0.39 (4)**	**0.17 (1)**	**-0.45 (4)**	**0.25 (2)**	-0.13 (sm)	0.03 (ns)	0.04 (ns)	-0.39 (4)	0.15 (wk)
8	Northwestness index (NWS)	-0.09 (ns)	0.09 (ns)	-0.16 (wk)	**-0.35 (4)**	0.1 (ns)	1	0.51 (4)	-0.17 (wk)	-0.02 (ns)
9	Cosine Aspect (CAS)	0.06 (ns)	0.05 (ns)	0.14 (wk)	**-0.28 (3)**	0.08 (ns)	0.51 (4)	1	0.16 (wk)	0.09 (ns)
10	Topographic Index	0.05 (ns)	0.07 (ns)	**0.27 (3)**	**-0.28 (3)**	0.08 (ns)	-0.17 (wk)	0.16 (wk)	1	0.03 (ns)
15	Slope (%)	**0.25 (2)**	-0.07 (ns)	-0.02 (ns)	0.02 (ns)	**0.23 (2)**	-0.02 (ns)	0.09 (ns)	0.03 (ns)	1

Table 3–B continued.

Rank	variable	3. RDL	4. TSE	5. VPD.April	6. Temp.April	11. TMX	12. PWM	13. T.MinJa	14. VPD.F
E.D	Environmental dissimilarity to mature forest	0.04 (ns)	0.13 (sm)	**0.5 (4)**	**0.21 (1)**	**-0.18 (1)**	-0.01 (ns)	-0.16 (wk)	**0.39 (4)**
23	MFI species cover in mf plot* (MFIcov mf)	**-0.45 (4)**	-0.08 (ns)	**-0.21 (1)**	0.17 (wk)	0.16 (wk)	**0.37 (4)**	**0.33 (4)**	-0.14 (wk)
22	DMFE	0.01 (ns)	-0.02 (ns)	**0.28 (3)**	**0.28 (3)**	-0.06 (ns)	0.01 (ns)	0.09 (wk)	0.17 (1)
1	Age (years)	0.12 (sm)	0.07 (ns)	**-0.25 (2)**	-0.09 (ns)	0.17 (1)	-0.16 (wk)	**0.46 (4)**	**-0.45 (4)**
2	Carbon-Nitrogen ratio (CN)	**-0.28 (3)**	0.07 (ns)	**0.19 (1)**	-0.12 (sm)	-0.14 (wk)	**0.31 (4)**	**-0.36 (4)**	**0.25 (2)**
7	Soil pH	0.08 (ns)	-0.04 (ns)	0.06 (ns)	-0.02 (ns)	-0.13 (wk)	0 (ns)	0.04 (ns)	-0.13 (sm)
3	Radiation lowest week (RLW)	1	**0.49 (4)**	-0.03 (ns)	**-0.37 (4)**	0.07 (ns)	-0.93 (4)	-0.12 (sm)	-0.11 (ns)
4	Temp seasonality (TSE)	**0.49 (4)**	1	0.01 (ns)	**-0.23 (2)**	0.4 (4)	-0.43 (4)	-0.02 (ns)	0.11 (ns)
5	VPD April mean (VPD.April)	-0.03 (ns)	0.01 (ns)	1	**0.45 (4)**	-0.08 (ns)	-0.02 (ns)	**-0.27 (3)**	**0.87 (4)**
6	Temp April mean (TApril)	**-0.37 (4)**	**-0.23 (2)**	**0.45 (4)**	1	**0.38 (4)**	**0.21 (1)**	**0.52 (4)**	**0.48 (4)**
11	Annual Temp mean maximum (TMX)	0.07 (ns)	**0.4 (4)**	-0.08 (ns)	**0.38 (4)**	1	**-0.29 (4)**	**0.53 (4)**	**0.18 (1)**
12	Precipitation warmest quarter (PWM)	**-0.93 (4)**	**-0.43 (4)**	-0.02 (ns)	**0.21 (1)**	-0.07 (ns)	1	0 (ns)	0 (ns)
13	Temp January mean daily minimum (T.MinJa)	-0.12 (sm)	-0.02 (ns)	**-0.27 (3)**	**0.52 (4)**	**0.53 (4)**	0 (ns)	1	**-0.22 (2)**
14	VPD pm February mean (VPD.Feb)	-0.11 (sm)	0.11 (ns)	**0.87 (4)**	**0.48 (4)**	**0.18 (1)**	0 (ns)	-0.16 (wk)	1
8	Northwestness index (NWS)	**-0.29 (3)**	**-0.24 (2)**	-0.07 (ns)	0.39 (4)	0.07 (ns)	**0.26 (2)**	**0.29 (4)**	0.03 (ns)
9	Cosine Aspect (CAS)	**0.19 (1)**	**0.17 (1)**	0.09 (ns)	0.16 (wk)	0.07 (ns)	-0.22 (2)	0.16 (wk)	0.04 (ns)
10	Topographic Index (TIN)	**0.45 (4)**	0.09 (ns)	**-0.23 (2)**	**-0.34 (4)**	**-0.34 (4)**	**-0.35 (4)**	-0.11 (ns)	**-0.39 (4)**
15	Slope (%)	**-0.21 (1)**	-0.15 (wk)	**0.18 (1)**	0.14 (wk)	-0.06 (ns)	0.12 (sm)	-0.02 (ns)	0.15 (wk)

^ Rank order of variables most associated with assemblage based on results from stepwise regression analysis in DistLM

* MFI species cover in mf plot was correlated against the environmental variables within the associated regrowth plots.

symbols for *P*-Values: ns $P > 0.1$; sm $0.1 > P > 0.05$; wk $0.05 > P > 0.01$; 1 $P < 0.01$; 2 $P < 0.001$; 3 $P < 0.0001$; 4 $P < 0.00001$

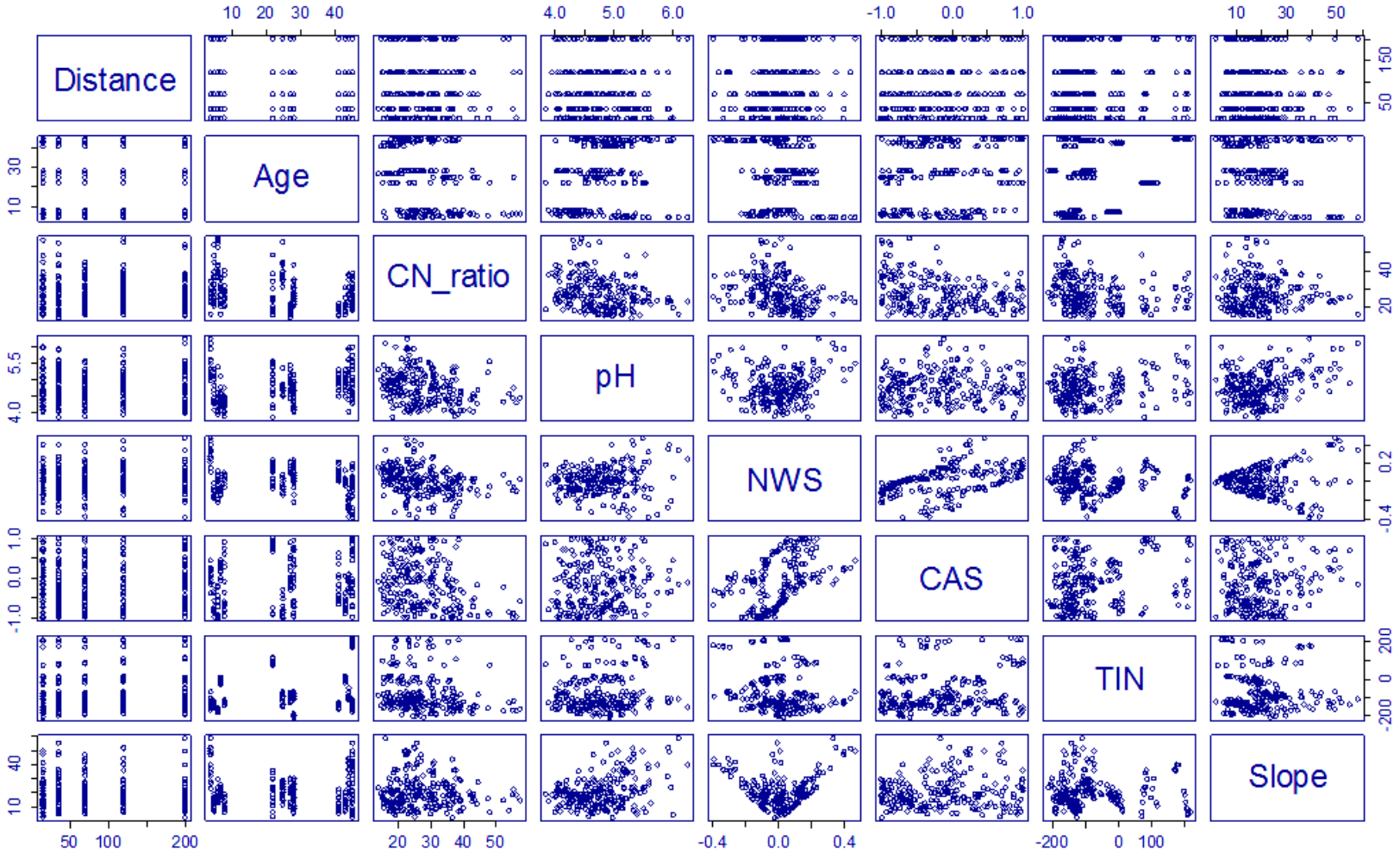


Figure 3-B. Matrix of scatter plots for selected variables (see Table 3–B for explanation of codes)

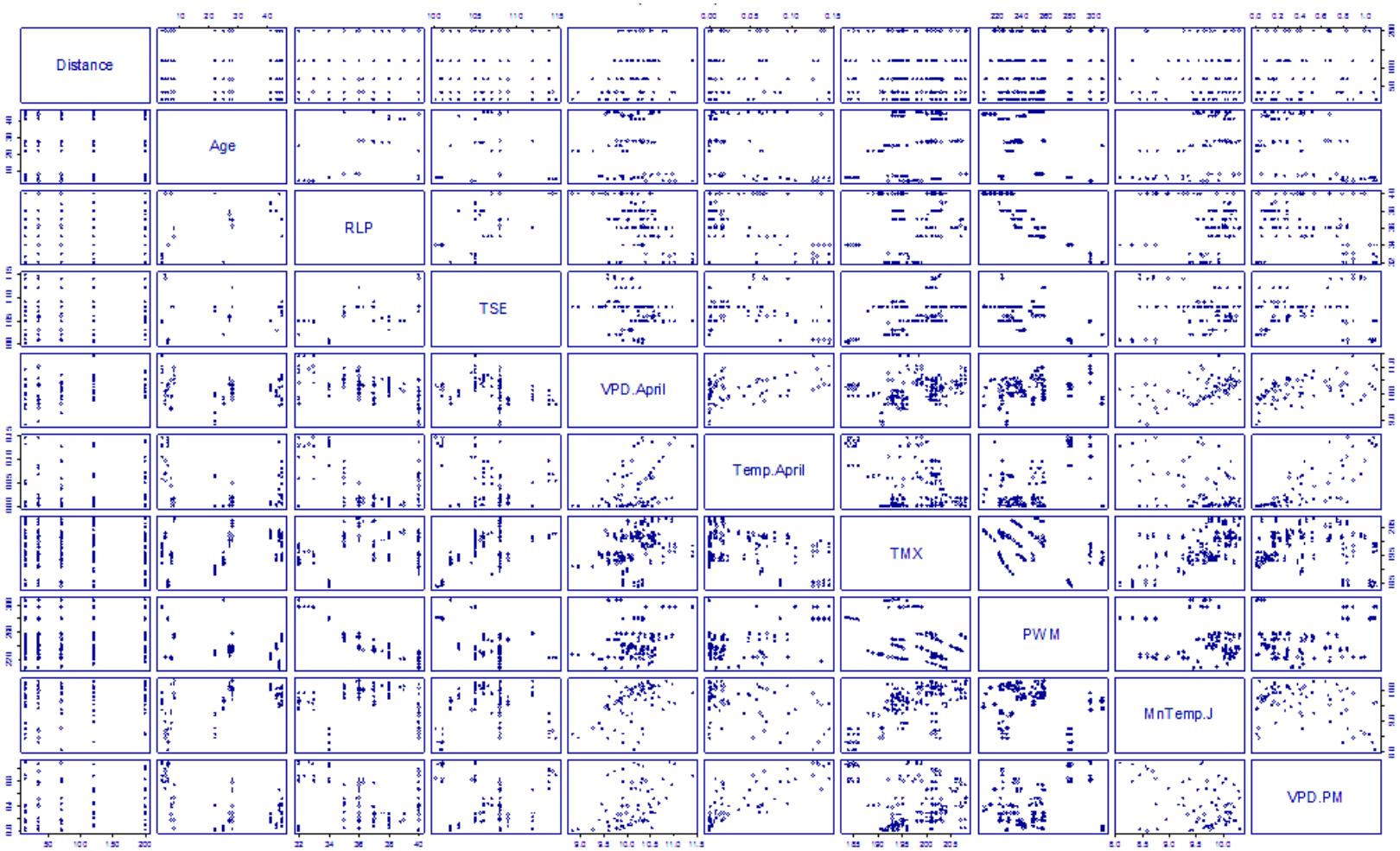


Figure 3–B. Continued.

3.2.2 Results of linear mixed effect and finite mixture modelling of floristic responses

Table 3-C. Summary of generalised linear model results for the mean (mu) and sigma response for seven floristic variables Data for each significant variable included in the model include the slope, ± standard error (t-value) and *P*-Value [Where sigma was modelled results are provided below those for mu; Table notes and abbreviations are provided below the table].

Floristic response variable	Fixed Effects:	Intercept	DMFE	Age	Climate^	Topography^	Other 1	Other 2	Other 3
Average Bray-Curtis dissimilarity to adjacent mature forest (square root transformed data)	LME (NO) BIC –391.0 R = 0.826 Random Effects sites	-0.3002 ± 0.0746 (t = -4.02) **mu** *** -4.252 ±1.983 (t = -12.82) **sigma** ***	**+** 0.0312 ±0.0097 (t = 3.22) log **	**-** 0.0053 ±0.0022 (t = -2.44) *		**+** 0.0028 ±0.0008 (t = 3.69) Slope ***	- 0.0875 ±0.0229 (t = -3.82) Coppice (+) ***	**+** 0.1970 ±0.0548 (t = 3.59) MFIcovMF *** 1.983 ±0.3705 (t = 5.35) MFIcovMF	**+** 0.0008 ±0.0004 (t = 2.24) log DMFE:age *
	LME(BE) -305.0 R = 0.895 Random Effects transects	-3.9852 ± 0.6512 (t = -6.12) **mu** *** 7.086 ±0.6406 (t = 11.06) **sigma** ***	**+** 0.0035 ± 0.0036 (t = 9.43) metres ***	-0.3441 ±0.1716 (t = -2.01)* m-stage -2.52 ±0.5432 (t = -4.65)*** y-stage	0.0670 ±0.0018 (t = 5.67) PWM.am ***	**+** 0.0139 ±0.0036 (t = 3.87) Slope ***		**+** 1.3143 ±0.2656 (t = 4.95) MFIcovMF *** -4.045 ±0.7156 (t = -5.654) MFIcovMF **	Range: -4.4473 ±0.5968 (t = -7.45)*** m4: to +4.7964 ±0.8943 (t = 5.36)*** y1:

Floristic response variable	Fixed Effects:	Intercept	DMFE	Age	Climate^	Topography^	Other 1	Other 2	Other 3
Average Bray-Curtis Dissimilarity to adjacent Mature forest continued	NP Finite Mixtures (NO) -357.7 R = 0.79 K= 2, site groups	0.4579 ± 0.0321 (t = 14.27) **mu** ***	**+** 0.0496 ±0.0065 (t = 7.60) log ***	**-** 0.0034 ±0.0004 (t = -7.85) age ***	-0.0017 ±0.0003 (t = -6.61) PWM .am ***	**+** 0.0036 ±0.0006 (t = 5.99) Slope ***	- 0.0751 ±0.0215 (t = -3.50) Coppice (+) ***		+ 0.1794 ±0.0142 (t = 12.61) Mass 2 ***
		-2.6675 ±0.0901 (-29.59) **sigma** ***		0.0111 ±0.0030 (t = 3.64) age ***					
	Effect size predicted Range used for predictions		*0.128* *15 – 200 m*	*0.136* *5-45 yrs*	*0.155* *215 to 305 mm*	*0.160* *5% to 50%*	*0.075* *+/-*		*0.179* *1/2*
Relative Cover of Mature forest Indicator Species	LME (BE) BIC= –538 R = 0.858 Random Effects sites	1.8317 ±1.1589 (t = 1.58) **mu** n.s.	-0.6401 ±0.0620 (t = -10.33) log ***	+0.0541 ±0.0193 (t = 2.8) *		-0.0162 ±0.0070 (t = -2.3) slope *	1.0863 ±0.1799 (t = 6.04) Coppice (+) ***	+1.5565 ±0.7199 (t = 2.16) MFIspp mf *	-0.3686 ±0.1637 (t = -2.25) pH *
		-0.1423 ±0.2690 (t = -0.53) **sigma** ns	-0.334 ±0.060 (-5.58) log ***	0.031 ±0.004 (t = 8.59) age ***		2.590 ±0.366 (t = 7.09) NWS ***			
	LME (BE) BIC= –391 R = 0.849 Random Effects transect	7.6485 ±1.4294 (t = 5.35) **mu** ***	-0.6250 ±0.0629 (t = -9.94) log ***	-0.1238 ±0.3522 (t = -0.35) n.s. m-stage 3.0063 ±1.1518 (t = 2.61)** y-stage	-0.0849 ±0.0255 (t = -3.34)) PWM.am **	-0.0172 ±0.0071 (t = -2.43) Slope *	1.0258 ±0.1844 (t = 5.56) Coppice (+) ***	-0.4053 ±0.1666 (t = -2.43) pH *	Range: -8.2779±1.9319 (t = -4.28)***y3: to 7.3026±1.2705 (t = 5.75) *** m4

Floristic response variable	Fixed Effects:	Intercept	DMFE	Age	Climate^	Topography^	Other 1	Other 2	Other 3
Relative Cover of Mature forest Indicator Species continued	LME (BE) BIC= –391 R = 0.849 Random Effects transects	-0.1798 ±0.2679 (t = -0.67) **sigma** n.s.	-0.3173 ±0.0596 (t = -5.32) log DMFE ***	0.0276 ±0.0035 (t = 7.8) age ***		2.3944 ±0.364 (t = 6.58) NWS ***			
	NP Finite Mixtures (BE) BIC= –516.9 R = 0.840 K= 2, site groups	1.208 ± 0.6465 (t = 1.87) **mu** #	-0.6517 ± 0.0640 (t = -10.19) log ***	24.8478 ± 1.3117 (t = 18.94)a.1*** -7.0266 ± 1.2403 (t = -5.67)a.2***	0.0358 ±0.0024 PWM.am ***	-0.0185 ± 0.0059 (t = -3.13) Slope **	1.1506 ± 0.1761 (t = 6.54) Coppice (+) ***	-0.4626 ± 0.1308 (t = -3.54) pH ***	1.3392 ± 0.1175 (t = 11.4) Mass 2 ***
		0.0009 ± 0.2696 (t = 0) **sigma** n.s.	-0.3564 ± 0.0600 (t = -5.94) log DMFE ***	0.0304 ± 0.0035 (t = 8.56) age ***		2.8607 ± 0.3665 (t = 7.81) NWS ***			
	Effect size predicted: Range used for predictions:		0-002 to 0.392	0.010 to 0.675	0.013 to 0.667	0.000 to 0.206	0.001 to 0.280	0.001 to 0.227	0.002 to 0.322
			15 – 200 m	5-45 yrs	215 to 305 mm	5% to 50%	+/-	4.0 to 6.0	1/2
Richness of Mature Forest Indicator Species	LME (PO) BIC = 994.9 R = 0.84	3.946 ± 1.7974 (t = 2.2) **mu** *	-0.0027 ± 0.0008 (t = -3.49) metres ***	-0.8289 ± 0.3622 (t = -2.29) mid * -0.5788 ± 0.3773 (t = -1.53) young ns	-0.5397 ± 0.1757 (t = -3.07) TApril **	-0.0036 ± 0.0012 (t = -3.1) TIN **		1.989 ±.5293 (t = 3.76) MFIcovMF ***	0.0013± 0.0011 (t = 1.20) DMFE. x.m- stage n.s -0.0042 ± 0.0015 (t = -2.75) DMFE.x. y-stage**

Floristic response variable	Fixed Effects:	Intercept	DMFE	Age	Climate^	Topography^	Other 1	Other 2	Other 3
	LME (PO) BIC = 1023 R = 0.847	1.4231 ± 0.6054 (t = 2.35) **mu** *	-0.0046 ± 0.0006 (t = -8.03) metres ***	-9.3674 ± 3.5434 (t = -2.64) A.1** 29.9951 ± 9.9474 (t = 3.02) A2**	-0.0527 ± 0.0139 (t = -3.8) PWM.am ***		0.0297 ± 0.0094 (t = 3.17) DMFE.X.age1** -0.0232 ±0.0076 (t = -3.05) DMFE.X.age2**	1.7537 ± 0.5389 (t = 3.25) MFIcovMF **	Sites: From y1:-2.751 ± 0.896 (t = -3.07) ** to: M4: 7.505 ±2.049 (t = 3.66)***
	NP Finite Mixtures (NO) BIC = 1069 R = 0.816	3.6615 ±0.8165 (t = 4.48) **mu** ***	-1.2697 ±0.1543 (t = -8.23) log ***	0.1288 ±0.0095 (t = 13.51) Age ***	0.0653 ±0.0056 (t = 11.61) PWM.am ***	-1.0371 ±0.2505 (t = -4.14)0 CAS ***	-0.0424 ±0.0136 (t = -3.12) Slope **		2.5533 ±0.3066 (t = 8.33) Mass 2 ***
		0.7221 ±0.1097 (6.58) **sigma** ***	-0.0023 ±0.0007 (t = -3.23) metres **	0.0096 ±0.003 (t = 3.16) Age **					
	Effect size predicted: Range used for predictions:		0 to 3.3 15 to 115	0 to 5.1 5 to 45	1 to 5.8 215 to 305	0 to 2.1 -99 to 99	0 to (1.7)1.9 5 to (45) 50 %		0 to 2.5 1:2
Total Species Richness	Linear Mixed Effects (NO) BIC = 1183.4 R = 0.515	0.6332 ± 0.5141 (t = -1.23) **mu** n.s	-0.0124 ± 0.0033 (t = -3.75) metres ***	7.56±3.60 (t = 2.10) A.1 * 9.49 ±3.44 (t = 2.76) A.2 ** -8.35±3.51 (t = 2.38) A.3 *	0.0376 ±0.0091 (t = 4.14) PWM.am ***	-1.3610 ± 0.3946 (t = -3.45) CAS ***			

Floristic response variable	Fixed Effects:	Intercept	DMFE	Age	Climate^	Topography^	Other 1	Other 2	Other 3
Shannon's H'	Linear Mixed Effects NO BIC =157.4 R = 0.59	-1.4659 ±0.5479 (t=) **mu** *	-0.0010 ±0.0003 (t=) metres **		0.0065 ±0.0014 (t=) PWM.am ***	0.1108 ±0.0519 (t=) CAS*	-0.9123 ±0.2400 (t=) NWS ***	0.1373 ±0.0565 (t=) MnTemp.J *	
Species Richness of Silvicultural Indicators	Linear Mixed Effects NO BIC = 1183 R = 0.51	-10.8971 ±3.1115 (t=) **mu** ***	ns	-0.0692 ±0.0100 (t=) Age ***	0.9296 ± 0.2865 TApril ***		-0.9999 ± 0.3562 (t=) Coppice (+) ***	0.6969 ±0.2456 (t=) pH ***	
Relative Cover of Silvicultural Indicators		4.7408 ± 1.3818 (3.43) **mu** ***	0.3061 ± 0.0604 (5.07) log ***	-0.0500 ± 0.0091 (-5.52) Age ***	-0.0190 ± 0.0052 (-3.68) PWM.am **		-0.5940 ± 0.1937 (-3.07) Coppice (+) **		
		1.2956 ± 0.4112 (t = 3.15) **sigma** **	0.329 ± 0.092 (t = 3.59) log DMFE ***	-0.036 ± 0.006 (t = -6.32) Age ***		-2.527 ± 0.585 (t = -4.31) NWS ***			

PWM.am: Precipitation in the warmest quarter above minimum (i.e. mm of rainfall above 207 mm in the warmest quarter)

DMFE: log— natural log of the distance to the mature forest edge, metres— Distance to mature forest edge in metres

Coppice two levels: - absent/ + present

Age = continuous variable in years; A1./A2./A3 Polynomial fit for age (first order, second order and third order respectively)

3 regrowth age classes l= late ~ 45 years; m= mid ~28 years; y= young ~ 5 years; For explanation of other codes see Table 3–B

3.2.2.1 Dissimilarity to adjacent mature forest

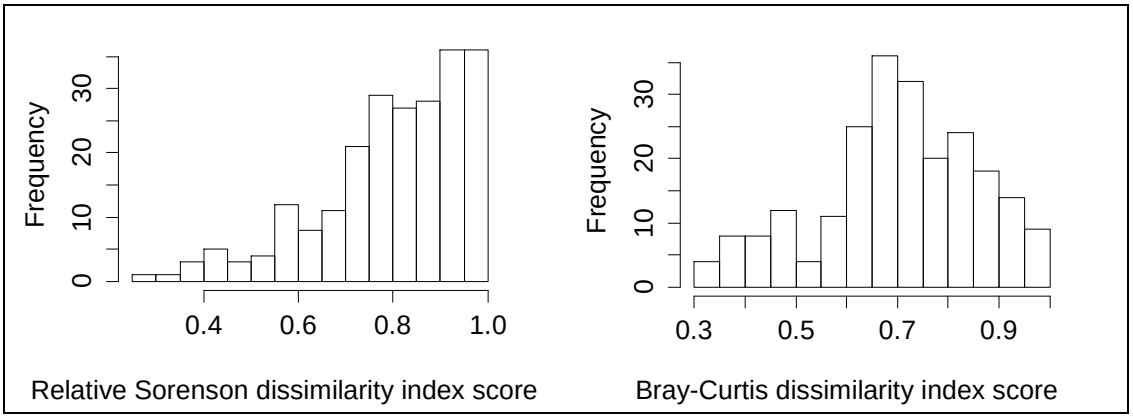


Figure 3-C. Distribution of the response average dissimilarity to adjacent mature forest based on resemblance matrices generated from (left) untransformed cover data; and (right) square root transformed cover data.

The distribution of the response variable, dissimilarity to mature forest generated for relative cover data and square root transformed cover data had very different distributions (Figure 3-F). Taking into account the structure in the data (random effects of sites) the Relative Sorenson dissimilarity data provided a better fit for a One inflated beta distribution (BIC = -335) compared with the Bray-Curtis dissimilarity based on square root transformed data to the normal distribution (BIC = -283.3), which failed the assumption of equal variance across the sampled range. Nevertheless, the latter variable provided a simpler model for interpretation, and there was only minor differences in model outcomes overall.

The mean for the Bray-Curtis dissimilarity to the nearest mature forest was 0.70. The ten highest ranking predictors for dissimilarity to mature forest using Random Forests were mean February afternoon VPD, rainfall in the warmest quarter, mean daily April temperature, average cover of mature forest indicator species in mature forest plots, topographic index, relative environment dissimilarity to mature forest plot, temperature seasonality, cosine of aspect, mean daily VPD for April, and percentage slope.

Both the random effects of sites and transects individually contributed to the reduction in model deviance compared with a null model, but there was no evidence to support the need for both. As site explained a greater amount of the variance in the response,

the model development proceeded, taking into account the random effects of site alone.

The gamlss linear mixed effect model incorporating the random effects of sites provided evidence that the interaction term between log transformed DMFE and age, age, coppice and percentage slope were all associated with the response variable (M1, Table 3–D).

Table 3-D. Summary of BIC results for iterative model development for the response variable 'Bray-Curtis dissimilarity to adjacent mature forest' using linear mixed effect modelling (based on resemblance matrix for square root transformed cover data)

Model	Mu formula (fixed effects)	Random effects	Sigma formula	BIC
M0(NO)	1	nil	1	-189.6
M0 (BEOI)	1	nil	1	-191.1
M0S (BEOI)	1	site	1	-267.7
M0S(NO)	1	site	1	-283.3
M0T (NO)	1	transect	1	-239.6
M0ST (NO)	1	site/transect	1	-258.9
MA (NO)	age (n.s)	site	1	(-283.4)
MD (NO)	log.DMFE	site	1	-332.0
MAD (NO)	age*log.DMFE (n.s.)	site	1	(-334.6)
M1 (NO)	log.DMFE*age + coppice + slope	site	1	-366.9
M2 (NO)	EnvDis to mf plots + MFIspp cover in mf plot	site	1	-336.9
M3 (NO)	age*log.DMFE + coppice + slope MFIspp cover mf plot	site	1	-375.1
M4 (NO)	age*log.DMFE + coppice + slope MFIspp cover in mf plot +EnvDis to mf plots	site	1	-381.8
M5 (NO)	age*log.DMFE + coppice + slope MFIspp cover mf plot	site	MFIspp cover mf plot	-391.0
FSM1 (NO)	site + log.DMFE*age + coppice + slope + rainfall.warmest.quarter	transect	MFIspp cover mf plot	-305.0
FSM2 (BEOI)	AgeClass/site + log.DMFE + slope + rainfall.warmest.quarter + MFIspp cover mf plot	transect	MFIspp cover mf plot	-311.4
FSM3 (BEOI)	AgeClass/site + DMFE + slope + rainfall.warmest.quarter + MFIspp cover mf plot	transect	MFIspp cover mf plot	-318.1

Abbreviations: n.s. = term not significant at the alpha level of 0.05

DMFE (either raw or log transformed) fitted in the model in the absence of age. However, age could only be fitted if the interaction between age and DMFE was included together with a formula for sigma that included age or MFI species cover in mature forest plots. This provided evidence that model precision declined with increasing regrowth age, and that the forests closer to the edge became increasingly more similar to mature forest while those further away did not change as much in their dissimilarity as they aged. These results supported the hypothesis that DMFE does have an effect on the similarity of regrowth species assemblage to that of the nearest mature forest. Likewise it provides evidence that dissimilarity declines with age but it does so more quickly in areas closer to the mature forest edge.

There was also evidence to support the alternate hypothesis that the response variable was associated with both the environmental dissimilarity to mature forest and MFI species cover in adjacent mature forest plots (Table 3–D, M2). However, the BIC for M2 was weaker than for M1. The addition of MFI species cover in mature plot to the terms included in M1 led to a lower BIC (Table 3–D, M3). The autocorrelation between environmental dissimilarity and DMFE indicate that it may be inappropriate to include these terms together in one model. Nevertheless when tested there was evidence to support the addition of the term for environmental dissimilarity between the plot and adjacent mature forest (Table 3–D, M4). When the model for sigma was improved by replacing age with MFI species cover in mature plot the best model included the interaction between age and log DMFE, coppice, slope and MFI species cover in mature plot (Table 3–D, M5, BIC-391, Pearson's R = 0.826).

The relatively poor fit and the large variance observed in the random effects for sites suggested another predictor variable is required to better explain differences in the response among sites (data not shown). The Normal Q-Q plot for random effects of sites (Figure 3–G, top left) demonstrate that some sites lie outside the normally distributed range and may be better accounted for by modelling sites as either a fixed effect in which transects are included as a random effect, or by a Finite Mixtures approach to account for the apparent differences among sites. When sites were included as a fixed effect and transects as a random effect BIC scores were worse due to the inclusion of the large number of sites (Table 3–D, FSM1). However, with this approach it was possible to nest sites within age class and include the term rainfall in

the warmest quarter as an additional fixed effect term. When rainfall was included in the model either the term Coppice or MFI species cover in mature forest plot had to be omitted. Coppice provided a marginally poorer fit than MFI species cover in mature forest and so was omitted. The beta family distribution also provided a better fit to the data, but with this distribution family the log transformation of DMF became unnecessary (Table 3–D, FSM3). The correlation between observed versus predicted values for the best model (FSM3) reached Pearson's R of 0.875.

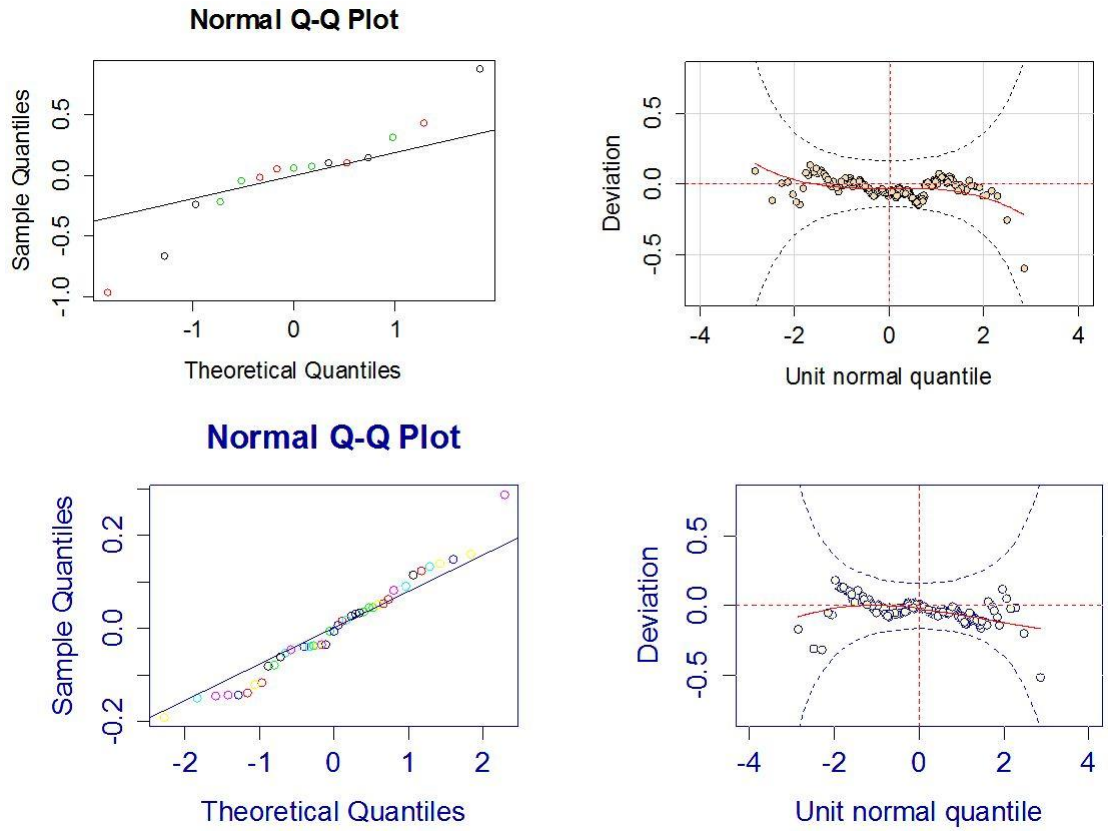


Figure 3-D. Random effect terms (left) and diagnostic wormplot of residuals (right) for linear mixed effect model 'M5' (top row) and 'FSM2' (bottom row) for Bray Curtis dissimilarity to mature forest.

There was evidence using Finite Mixtures modelling, that three site groups could be justified for modelling Bray-Curtis dissimilarity to mature forests without including other terms in the model for mu (Table 3–E). With the addition of DMFE and other terms for mu, no more than two site groups were required.

Table 3-E. Deviance for Finite Mixture models of Bray-Curtis dissimilarity to mature forest specifying different number of mass points for site groups (normal family distribution)

Ki	df	Deviance squared	Δ in Deviance	BIC	Δ in BIC
1	2	-200.5	na	-189.6	n.a.
2	4	-292.4	-92.0	-268.0	-78.4
3	6	-323.5	-27.5	-280.8	-12.8
4	8	-323.7	- 0.2	-269.1	11.7

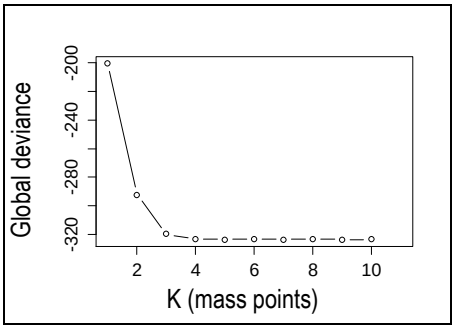


Table 3-F. Some iterative stages of model development using Finite Mixtures modelling for Bray-Curtis dissimilarity to mature forest (family=Beta, logit link function for mu and sigma, K=2)

Model	Formula Mu	Formula sigma	DF	BIC
0	1	1	4	-268.0
1	DMFE		5	-295.0
2	age	1	5	-261.9
3	DMFE + age	1	6	-273.7
4	DMFE*age (n.s.)	1	7	(268.3)
5	Log DMFE* age+ rain.warm quarter+coppice + slope	1	10	-350.0
6	Log DMFE + age+ rain.warm quarter+coppice + slope	1	10	-354.7
7	Log DMFE + age+ rain.warm quarter+coppice + slope	age	11	-357.7

Bray-Curtis dissimilarity to mature forest was associated with regrowth forest age and there was evidence that the model precision reduced with increases in regrowth age (Table 3–F). Age and DMFE included together in the model provided a better fit to the data than either variable on its own, but the interaction term weakened the model strength (Table 3–F).

The best model (Model 7, Table 3–F) included log DMFE, age, slope, rainfall in the warmest quarter and coppice in the formula for mu, and age within the formula for sigma. The correlation between observed and fitted values for model 7 had Pearson's R of 0.79. The posterior probabilities of membership for each site group were close to 1 for all plots. When the post-posterior probabilities were fitted for membership only, four sites were assigned to the first group of mass points (L5, KD43H; M4, PC39F; Y1, DN07A; Y3, FN23E).

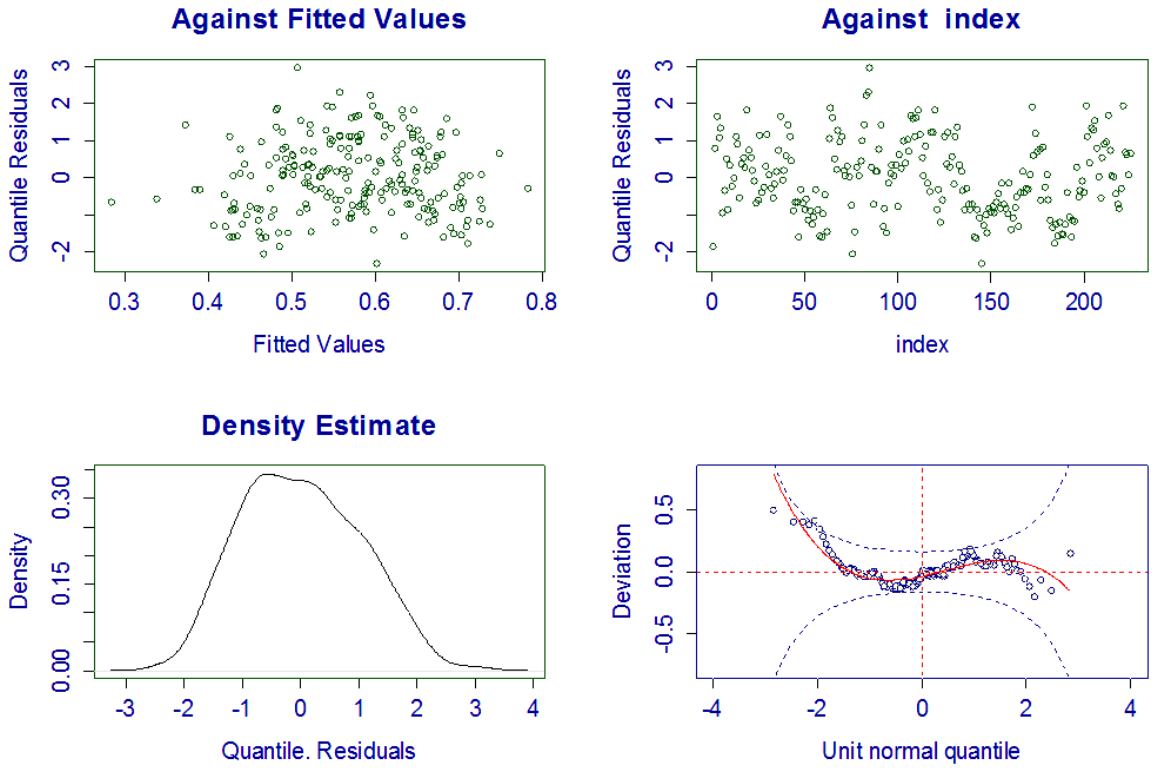


Figure 3-E. Diagnostic residuals plots (including worm plot, bottom right) for Finite Mixtures model 'M6'for Bray Curtis dissimilarity to mature forest.

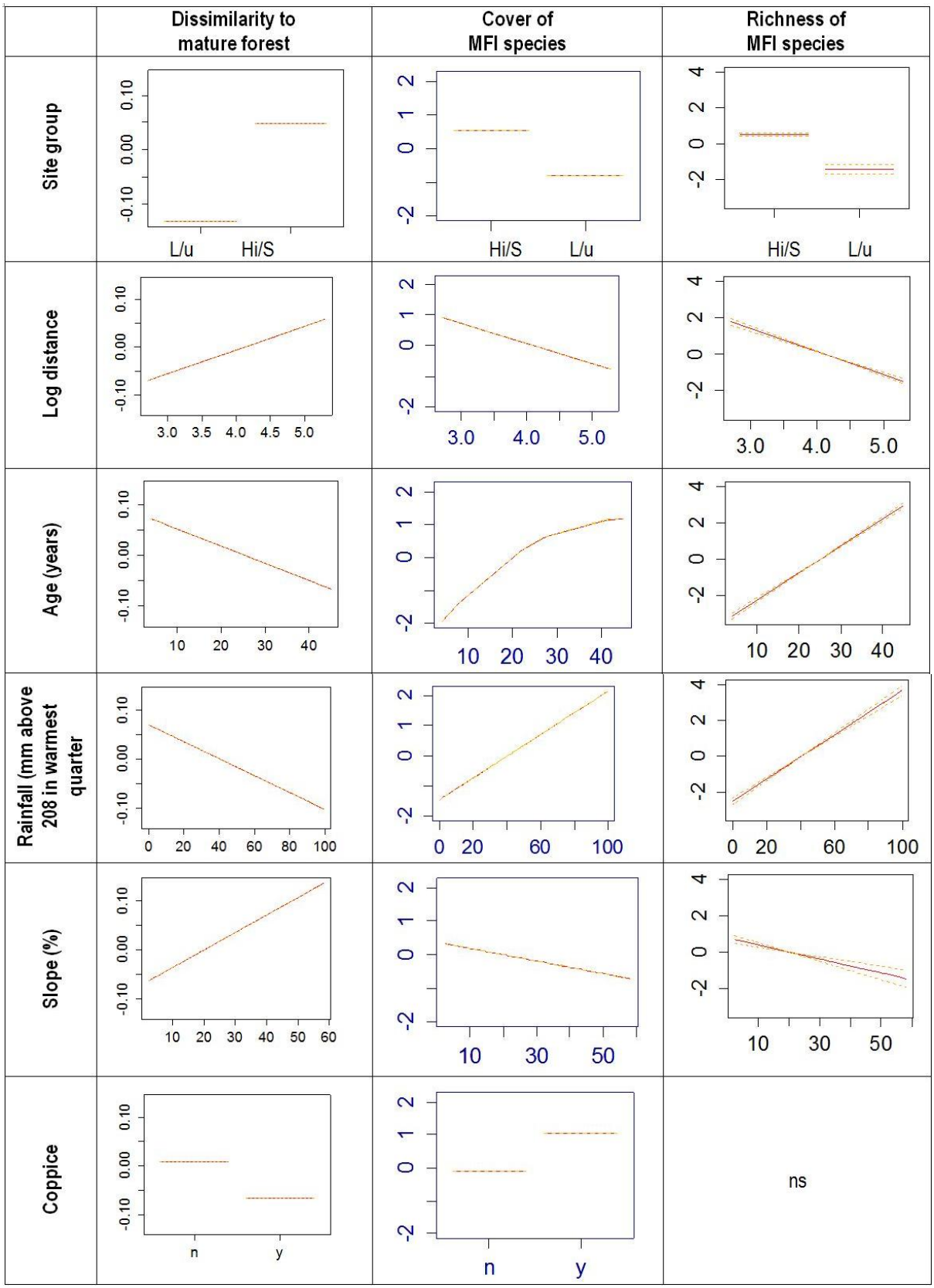


Figure 3-F. Predicted partial response for three floristic variables (y axis) to each predictor (named in left column) across the sampled range of the predictor (x-axis). Continued over page ...

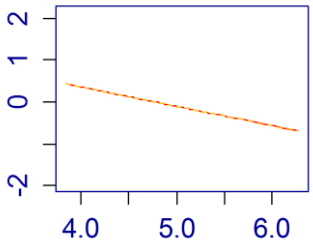
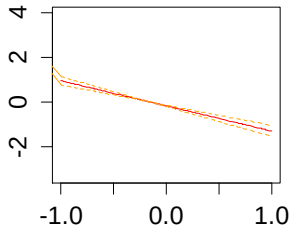
	Dissimilarity to mature forest	Cover of MFI species	Richness of MFI species
Soil pH	ns		ns
Cosine of aspect	ns	ns	

Figure 3-F continued. Predicted partial response for three floristic variables (y-axis) to each predictor (named in left column) across the sampled range of the predictor (x-axis). Predictions derived from generalised linear models developed using predicted values from Finite Mixtures models based on the random effects of two site groups.

Abbreviations and units

Site group: Hi/c: Sites with higher response, most common site type;
L/u Sites with lower response less common site type;

log distance: natural log of distance to nearest mature forest edge (m)

Coppice: Y: present, N: absent.

3.2.2.2 Relative cover of mature forest indicator species

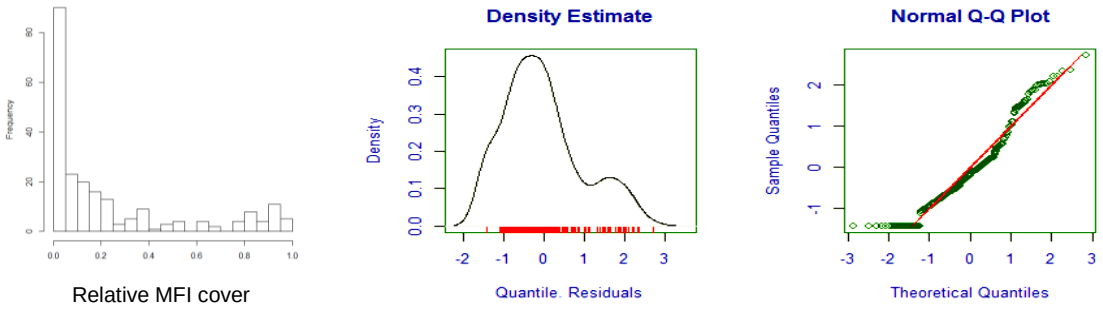


Figure 3-G. Frequency histogram of relative cover of mature forest indicator species (left) and diagnostic residual plots for beta distribution (middle and right).

The beta distribution family was found to provide the best fit to the untransformed cover of MFI species (BIC (NO) = 111; BIC (BE) = -312). There was still some evidence for non-normal bimodality among the residuals when the nested structure in the data wasn't accounted for (Figure 3-).

The variables best predicting the abundance of MFI species using Random Forests were: rainfall in the warmest quarter, age, mean afternoon VPD for February, Radiation of the lowest period, cosine of aspect, topographic index, mean daily temperature for April, temperature seasonality and the average relative cover of mature forest indicators species in the adjacent mature forest patch. Using the drop term functions in gamlss the predictors with greatest association were log DMFE, age, rainfall, mean minimum January temperature, presence of coppice, soil pH, fire frequency, mean daily temperature in April and northwestness. After taking into account the random effects of sites, mixed effect modelling demonstrated a negative association between the cover of MFI species and log DMFE and a positive association with both age and coppice. For this model of mu the best model for sigma provided evidence that variance in cover of MFI species increased with regrowth age and northwestness and declined with increasing DMFE. The model for Mu also improved with the addition of northwestness but as the coefficient provided evidence that mature forest increased in association with increased northwestness in contradiction to ecological theory it was omitted from the main model, ultimately MFI species cover in mature forest, slope and pH provided better additions for the model of mu (Table 3–G, M7). The Pearson correlation for this model was 0.849. By adding sites as a fixed effect using mixed effect modelling, the

association between MFI species cover and rainfall was demonstrated (Table 3–G, M8, Table 3–C).

Table 3-G. Summary of model development stages for linear mixed effects models of relative cover of mature forest indicators (family =beta, logit link for sigma and mu)

Model	Mu formula fixed effects	Mu random effects	Sigma formula	BIC for BE
M0	1	nil	1	-312.9
M0rT	1	transect	1	-316.1
M0rST	1	site/transect	1	-365.1
M0rS	1	site	1	-406.7
M1	Log DMFE + age + coppice + rain.m + pH	site/transect	1	-423.5
M2	Log DMFE + age + coppice + rain.m	transect	log DMFE + age + NWS	-447.6
M3	Log DMFE + age + coppice + rain.m	site/transect	log DMFE + age + NWS	-477.1
M4	Log DMFE + age + coppice + rain.m	site	log DMFE + age + NWS	-518.6
M5	Log DMFE + coppice +age+ rain.m+ MFIcov mf plot	site	log DMFE + age + NWS	-522.3
M6	Log DMFE + coppice + MFIcov mf plot +[environ. dissimilarity to mat plots #]	site	log DMFE + age + NWS	[-526.1]
M7	Log DMFE + coppice + MFIcov mf plot + slope + pH	site	log DMFE + age+ NWS	-538.1
M8	Site nested in age + log DMFE + coppice +slope +pH + rain.m	transect	log DMFE + age + NWS	-522.6

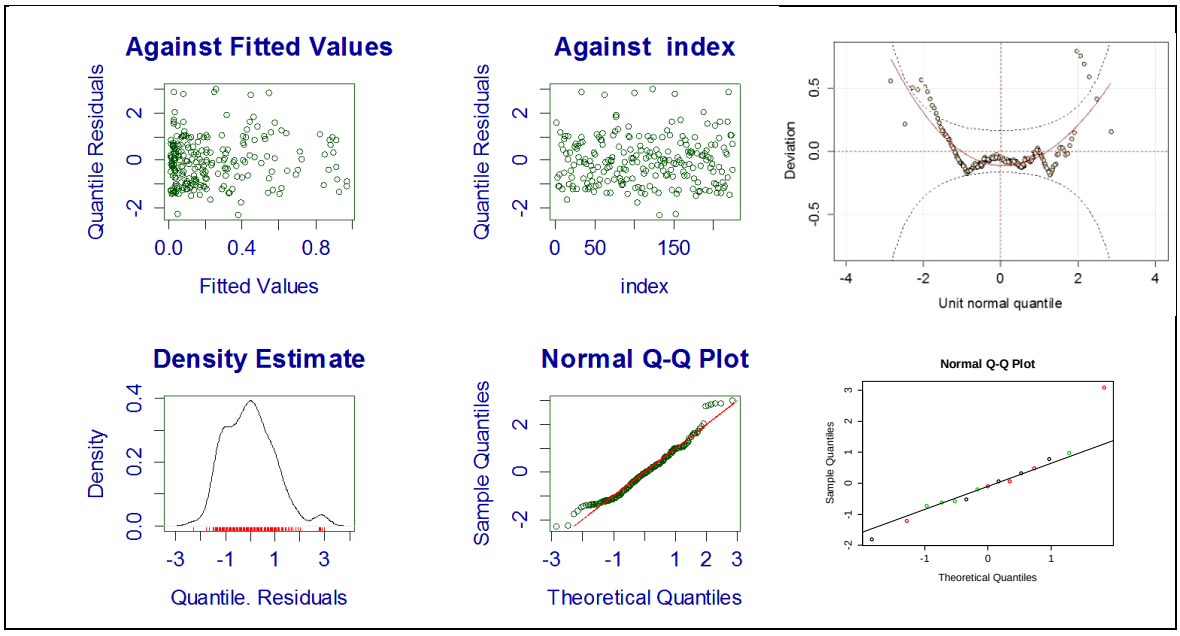
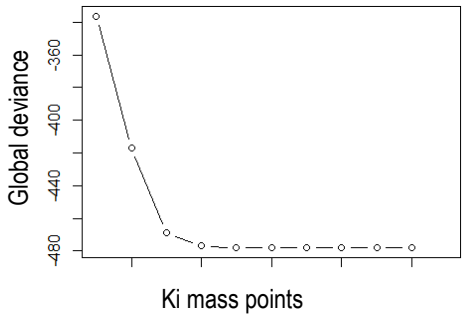


Figure 3-H. Diagnostic residual plots for best linear mixed effect model of cover of MFI species (Table 3–G, M7); QQ plot of random effects of sites located bottom right.

Finite Mixtures analysis was undertaken to compare results between approaches. Cover of MFI species varied sufficiently between sites that a Finite Mixtures analysis with three mass points may have been justified (Table 3–H). However, with the addition of variables to the model two site groups provided optimal results. The final best model differed from that produced using mixed effects modelling only by omitting MFI species cover in mature forest plot, including rainfall and adding a second order polynomial term for age (Table 3–C). The correlation of the fitted values with observed for the Finite Mixtures model was only marginally less than the mixed effects model (R = 0.84, BIC -516.9). The fitted values for the models from both methods had a very high correlation with each other (R = 0.99).

Table 3-H. Deviance for models of relative cover of MFI species specifying random effects for different number of site groups (Ki) together with model development stages below.

Ki	df	Deviance squared	Δ in Deviance	BIC	Δ in BIC
1	3	-336.1	336.1	-319.9	
2	**5**	**-428.1**	**-92.1**	**-390.0**	**-80.1**
3	**7**	**-469.0**	**-40.9**	**-431.0**	**-41.0**
4	9	-476.8	-7.8	-428.1	+2.9
5	11	-478.0	-1.2	-418.5	+9.6
>5	>11	-478.0	±0.05	>-408.5	>10



Model development

Model	Mu formula fixed effects	Mu random effects	Sigma formula	BIC for BE
M0 (BE)	1	Site (Ki=2)	1	-372.7
MD (BE)	DMFE	Site (Ki=2)	1	-386.5
MA (BE)	Age	Site (Ki=2)	1	-370.4
MA2 (BE)	Poly(age,2)	Site (Ki=2)	age	-374.5
MAD (BE)	DMFE+Age	Site (Ki=2)	1	-383.0
M1 (BE)	Log DMFE + age + rainfall wm.Q. + pH + coppice	Site (Ki=2)	1	-453.3
M2 (BE)	Log DMFE + age + rainfall wm.Q. + pH + coppice	Site (Ki=2)	logDMFE+ Age+NWS	-503.5
M3 (BE)	Log DMFE + poly(age,2) + rainfall wm.Q. + pH + coppice	Site (Ki=2)	logDMFE+ Age+NWS	-514.6
M4 (BE)	Log DMFE + poly(age,2) + rainfall wm.Q. + pH + coppice+Slope	Site (Ki=2)	logDMFE+ Age+NWS	-516.9

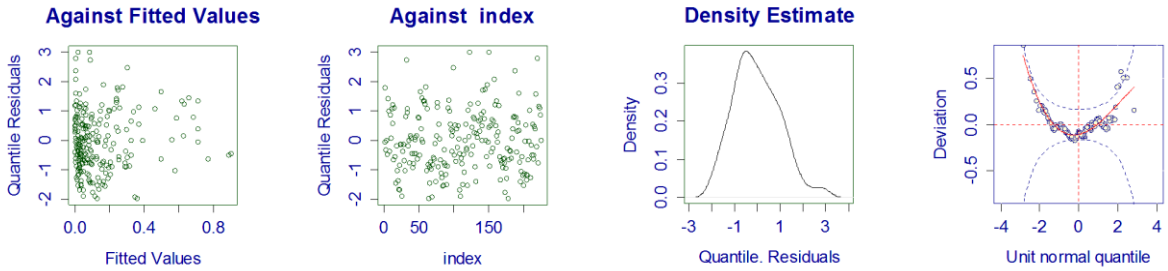


Figure 3-I. Diagnostic residual plots for the Finite Mixtures model for the relative cover of mature forest indicator species in regrowth forest (family = beta, logit link function for both mu and sigma, and k=2 mass points).

3.2.2.3 Mature Forest Indicator Species Richness

The Poisson distribution provided a marginally lower BIC compared with the negative binomial distribution for richness of MFI species (Table 3–I). The predictors with greatest importance value for predicting MFI species richness using Random Forests were age and mean VPD for February afternoons. Other variables of much lower importance were mean daily temperature for April, rainfall in the warmest month, mean daily VPD for April, topographic index, radiation in the lowest week, cosine of aspect, temperature seasonality and mean minimum January temperature. DMFE was ranked 13th among the site predictors tested.

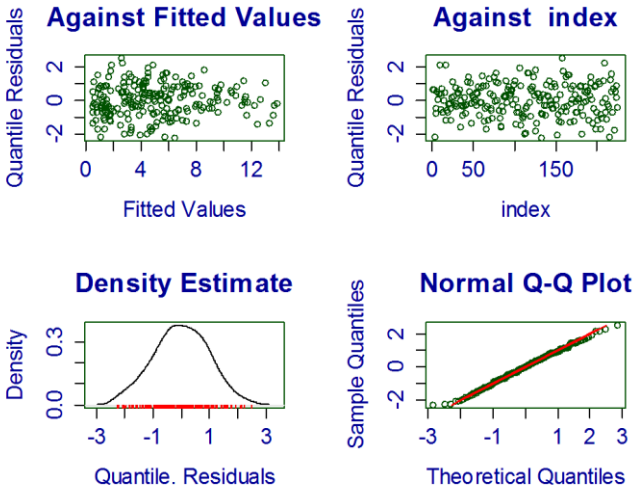
When the random effects of sites were taken into account using a linear mixed effect model, MFI species richness proved to be negatively associated with DMFE, northerly aspects, topographic index and mean April temperatures and positively associated with age (M1, Table 3–I). The environmental dissimilarity of the plot to mature forests and MFI species cover in mature forest plot were also associated with MFI species richness and remained so when the other predictors were included with them (Table 3–I, M2, M3). The final model best included MFI species cover together with DMFE, age class, the interaction between DMFE and age class, topographic index and mean April temperature, but it omitted cosine of aspect (Table 3–I:M5). The Pearson correlation between predicted versus observed richness of MFI species was R= 0.843.

When the model was modified to include sites as a fixed effect, the interaction between age class and DMFE remained a valuable predictor but mean April temperature and topographic index were omitted in favour of rainfall in the warmest quarter (Table 3–I, M2, M3). The correlation of the fitted values was much the same R = 0.847. The marginal improvement in the predictions did not justify the increased model complexity of this approach and the lack of improvement in the distribution of residuals (Table 3–I).

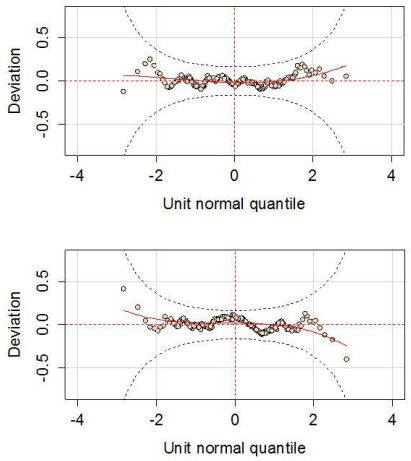
Table 3-I. Summary of model development stages for Mature forest indicator species richness using linear mixed effect modelling

Model	Formula Mu	Random effects	Sigma	DF	BIC
normal	1	site	1	15	1123.9
Zero Inflated Poisson	1	site	1	15	1109.4
negative binomial	1	site	1	15	1106.1
poison	1	site	1	15	1104.6
MA(PO)	Age	site	1	15	1095.9
MD (PO)	DMFE	site	1	15	1048.7
MAD (PO)	Poly(TSLF,2)*DMFE	site	1	15	1038.5
M1(PO)	DMFE + age + cos aspect +topographic index + mean daily April temperature	site	1	15	1017.6
M2(PO)	Environmental dissimilarity to mat plots + MFIcover in mf plot	site	1	16	1026.9
M3(PO)	DMFE + age + cos aspect +topographic index + mean daily April temperature+ MFIcover in mf plot	site	1	16	1008.3
M4(PO)	DMFE + age + cos aspect +topographic index + mean daily April temperature+ MFIcover in mf plot + Environmental dissimilarity to mat plots	site	1	16	1006.2
M5(PO) R=0.843	DMFE* age class+ topographic index +mean daily April temperature +MFIcover in mf plot	site	1	16	994.9
M6(PO) (R = 0.847)	DMFE*age class + rainfall in warmest quarter +MFIcover in mf plot	transect	1	19	1023.7

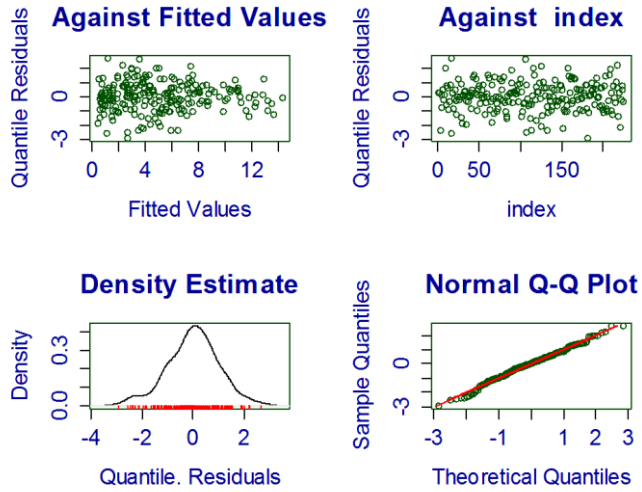
Using Finite Mixture modelling for the richness of MFI species BIC scores were lower for the best models developed using Poisson distribution than the normal distribution. Nevertheless the diagnostic plots of the residuals were better distributed using the normal distribution. When modelling with a Poisson distribution there was evidence of an interaction effect with a second order polynomial for regrowth age but the increased complexity of the model was not justified by the BIC scores. The simplest models under both distributions included log transformed DMFE, regrowth age, cosine of aspect and rainfall in the warmest quarter. Slope also contributed to model improvement when modelled with a normal distribution. Using the normal distribution the model was also improved by the addition of sigma terms for distance and age, demonstrating that the variance of species richness was not uniform across the sampled range (Table 3–J, FM2). The best model using a normal distribution had a Pearson's correlation between the observed versus predicted of R = 0.816.



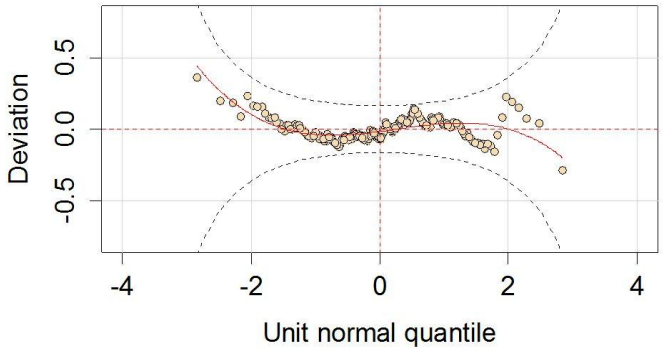
MFI species richness linear mixed effect Model 5 (Poisson): sites as random effects



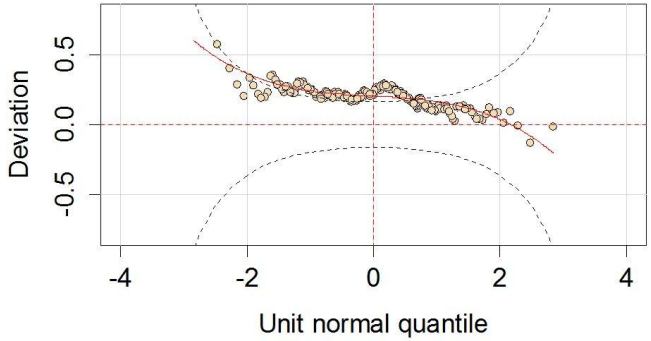
Worm plots linear mixed effect Model 5 (top)
& LME Model 6 (bottom)



MFI richness linear mixed effect Model 6 (Poisson): sites included as fixed effects and transects as random effects



Diagnostic Residual Worm plot for FM2(Normal)



Diagnostic Residual Worm plot for FM3(Poisson)

Figure 3-J. Residual diagnostic plots for MFI species richness models analysed using linear mixed effect modelling (above) and Finite Mixtures modelling (lower)

Seven of the 15 sites were assigned to the first site group using the Finite Mixtures approach with the probability of group membership being close to one for the majority of plots and greater than 0.9 for a few. The first site group had lower mature forest indicator species richness values compared with the second site group.

Table 3-J. Summary of model development stages for Mature forest indicator species richness using the Finite Mixtures method

Model	Formula Mu	Sigma	Random effects	DF	BIC
FM0a(PO)		1	1|site, k=1	2	1418.4
FM0b(NO)		1	1|site, k=1	2	1253.7
FM0b(NO)	1	1	1|site, k=2	4	1160.7
FM0c(NO)	1	1	1|site, k=3	6	1130.5
FMD(NO)	logDMFE	1	1|site, k=2	5	1127.1
FMA1(NO)	Age	1	1|site, k=2	5	1153.7
FMDA(NO)	logDMFE+age	1	1|site, k=2	6	1118.7
FM1(NO) R=0.816	logDMFE + age + cos aspect +slope +rain in warmest quarter	1	1|site, k=2	9	1072.9
FM2(NO) R=0.816	**logDMFE + age + cos aspect +slope +rain in warmest quarter**	**Age+DMFE**	**1|site, k=2**	**11**	**1068.6**
FM3(PO) R=0.809	logDMFE + age + cos aspect +rain in warmest quarter	1	1|site, k=2	8	1046.7
FM3(NO) R=0.808	logDMFE + age + cos aspect +rain in warmest quarter	Age+DMFE	1|site, k=2	10	1071.7

3.2.2.4 Species richness

Species Richness, S, was best fitted with a normal distribution, although before taking into account the nested structure in the data a negative binomial distribution provided a similar fit (Table 3–K). Using Random Forests, best predictors of species richness from among the site variables were cosine of aspect, topographic index, northwestness, slope and rainfall in the warmest quarter. There was no evidence that variation between sites justified the use of a Finite Mixtures approach for this response variable. There was also no evidence within this data set that species richness changed sufficiently with regrowth age to justify the inclusion of this parameter in the model unless a second or third order polynomial term for age was fitted. The results of the best mixed effects model (M4,Table 3–K). The fitted values had a correlation with observed species richness of Pearson's R = 0.51.

Species richness was not associated with MFI spp cover in MF plot, although the P-value did approach the alpha level of significance. Although species richness was negatively associated with environmental dissimilarity to mature forest, neither variable contributed to an improvement in the model when other site variables such as DMFE were included).

The predicted decline in species richness in regrowth forest with DMFE was 2.3 species. The difference between observed values at 15 m, 35 m and 70 m from the edge could not be distinguished by chance variation, while the differences between observed values at 15 m from those at 120 and 200 m were unlikely to be due to chance variation ($P < 0.05$, data not shown). The predicted effect of distance was greater than age but smaller than both rainfall and aspect.

Table 3-K. Summary of model development stages for the response variable Species Richness using linear mixed effect modelling

Model	Formula Mu	Random Effects	DF	BIC
Family normal	1	1		1245.8
Family negative binomial	1	1		1246.5
Family Gamma	1	site		1256.1
Family NBI	1	site		1254.9
M0a: normal	1	site		1246.0
M0b: normal	1	transect	29	1304.2
M0c: normal	1	site/transect	19	1263.1
M1 normal	age + age.squared +Log distance + rain in warmest quarter (minus minimum)+ cos.aspect	site/transect	16	1228.8
M2 normal	age + age.squared +Log distance + rain in warmest quarter (minus minimum)+ cos.aspect	site	5	1200.9
M3 normal	age + age^2+age^3+Log distance + rain in warmest quarter (minus minimum)+ cos.aspect	site	3	1192.8
M4 normal	age + age^2+age^3+distance + rain in warmest quarter + cos.aspect	site	3	1183.4
Malt normal	Environmental dissimilarity to mat forest	site	14	1236

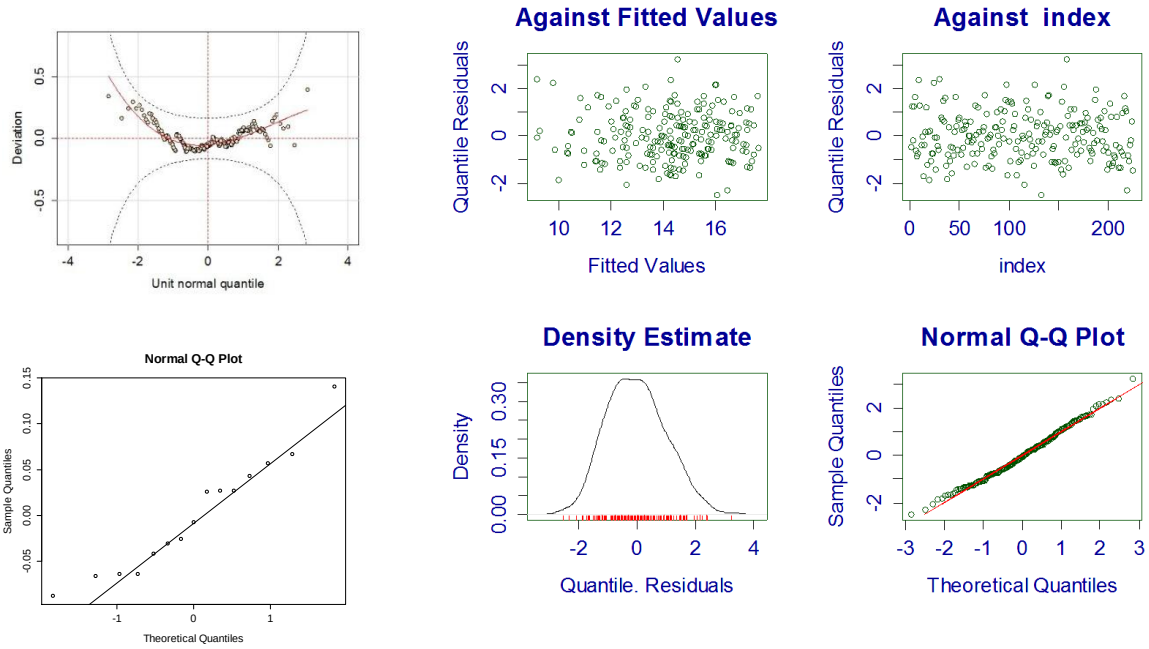


Figure 3-K. Residual plots for linear mixed effect model for species richness including the random effects of site (bottom left)

The model predicted that species richness in the late stage regrowth would have 1.9 species more than the mid-stage regrowth, but only 0.5 species more than young regrowth. The differences in observed richness between each age class were more different than could be explained by chance variation ($P < 0.05$, data not shown). Rainfall had the greatest predicted effect on total species richness, with an expected increase of 3.5 species across sampled gradient in rainfall (215 mm to 305 mm in the warmest quarter). The southerly aspects were predicted to have 2.8 more species than regrowth on northerly sites.

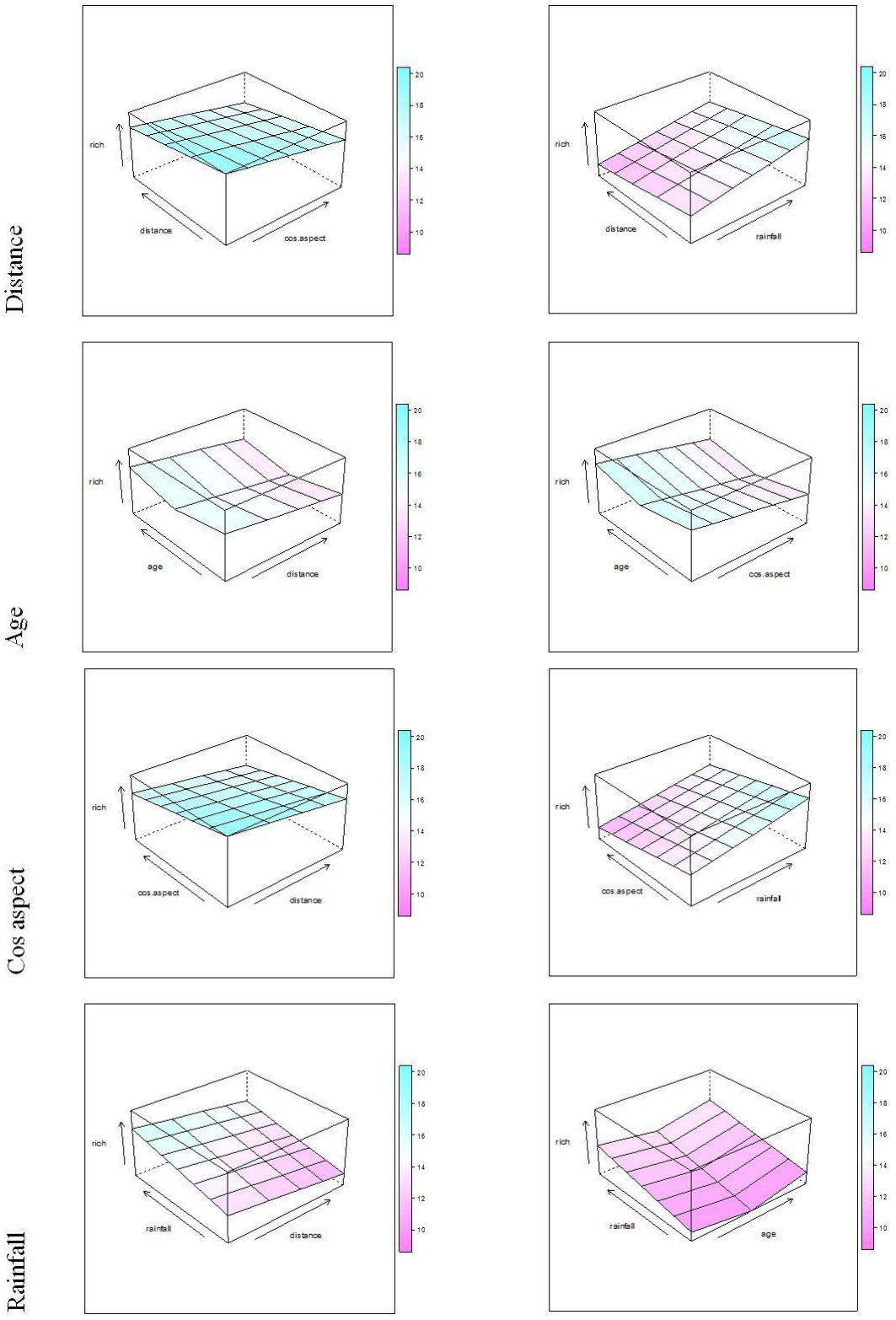


Figure 3-L. Predicted response of species richness (y-axis) to variation in the sampled gradient of distance from the mature forest edge (distance: 15, 35, 70, 120 and 200 m), regrowth age (age: 5 years; 25 years, 45 years old), aspect (cos apect, South to North), and rainfall in the warmest quarter (rainfall 215, 230, 255, 270, 285 and 305 mm).

3.2.2.5 Shannon's H'

Shannon's diversity index, H', the entropy value rather than the true diversity score, did not differ significantly from a normal distribution (Table 3-L, Figure 3-E). The variable best predicting this response using Random Forests was cosine of aspect. The other top ten in rank order were northwestness, topographic index, carbon-nitrogen ratio, rainfall in the warmest quarter, mean daily April temperature, slope, maximum temperature, annual temperature and soil pH. Distance ranked 15th and age 17th.

Using the linear mixed effects method to take account of the random effects of site the best formula for the prediction of Shannon diversity included the site variables DMFE, rainfall in the warmest quarter, northwestness, cosine of aspect and mean daily minimum temperature for January (Table 3-L). Shannon's H' increased with rainfall, more northerly aspects and higher mean minimum temperatures in January but declined in association with distance from the edge and northwestness. As cosine of aspect and Northwestness are positively correlated the inclusion of both variables in the model with coefficients with reverse signs provides evidence that one is correcting the fit of the other. A third order polynomial of northwestness was successfully fitted as an alternative to the inclusion of cosine of aspect. On its own cosine of aspect did not fit in the model, while northwestness did. This provides evidence that there is a non-parametric association between Shannon's H' and topography. There was no strong association between minimum January temperature and the other variables in the model and it was positively associated with the response when included with or without the other variables. Pearson's correlation for the fitted values from the best model with observed values was only 0.59. The diagnostic plots of residuals provided evidence of the robustness of the model, and no evidence that the random effects of sites warranted treating as separate site groups (Figure 3-D). The unexplained random effects of site differences were of the same order of magnitude as the predicted effects of the site variables with a difference in Shannon's diversity score H' of 0.35. In comparison the gradient in rainfall was expected to result in a variation of H' of 0.6, while the variation in northwestness after subtracting the counter balancing effect of aspect differences was predicted to result in a difference in H' of 0.5. Temperature variation contributed to a variation in H' of 0.3 while the

impact of distance from edge had the smallest predicted effect which on average resulted in a decline of H' of 0.2 between 15 m from the edge and 200 m.

Table 3-L. Summary of model development stages using linear mixed effects modelling for Shannon's H

Model	Formula Mu	Random Effects	DF	BIC
BCT	1	na		204.7
Gamma	1	na		216.1
Normal	1	na		196.4
0t:normal	1	transect		253.0
0s:normal	1	Site	4	196.4
0st:normal	1	Site/transect	5	220.3
1 normal	distance	Site	14/209	184.0
2 normal	age	Site	14/209	n.s
3 normal	Distance + rain in warmest quarter + Cos aspect + Northwestness + mean daily minimum temperature in January	Site	6	157.4
4 normal	Relative environmental difference + rc mature species in mat plots	Site		ns

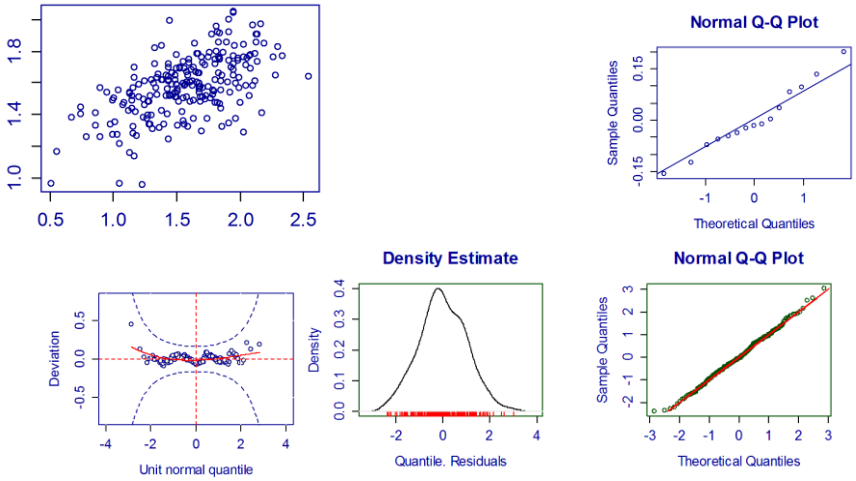


Figure 3-D. Model results for linear mixed effect M3 for Shannon's H', Pearson's R =0.59: Observed versus predicted (top left), random effect of sites Q-Q plot (top right) and diagnostic residual plots (bottom row)

3.2.3 Descriptive statistics for three responses

Table 3-M. Summary statistics for three response variables used to predict magnitude of the effect of DMFE in wet eucalypt forest

Variable	Treatment	N	N*	Mean	SE Mean	StDev	Minimum	Q1	Median	Q3	Maximum
Dissimilarity to mature forest (Bray-Curtis, square root transformed data)											
	O-15	15	0	0.3838	0.0195	0.0757	0.2827	0.3290	0.3714	0.4282	0.5181
	O15	15	0	0.5981	0.0420	0.1626	0.3282	0.4529	0.6377	0.7121	0.8190
	O35	15	0	0.6528	0.0465	0.1802	0.3752	0.4598	0.6523	0.7725	0.9249
	O70	15	0	0.6979	0.0496	0.1923	0.4170	0.5235	0.6977	0.8614	1.0000
	O120	15	0	0.7173	0.0430	0.1664	0.4254	0.5759	0.6952	0.8579	0.9720
	O200	15	0	0.7551	0.0446	0.1729	0.4307	0.6279	0.7471	0.9107	0.9684
	M-15	15	0	0.3249	0.0202	0.0783	0.1590	0.2726	0.3304	0.3942	0.4625
	M15	15	0	0.5997	0.0404	0.1567	0.3329	0.4903	0.6409	0.7050	0.8254
	M35	15	0	0.6453	0.0434	0.1681	0.3443	0.4503	0.7024	0.7879	0.8968
	M70	15	0	0.7201	0.0427	0.1656	0.3574	0.6530	0.7995	0.8231	0.9255
	M120	15	0	0.7185	0.0460	0.1780	0.3876	0.6757	0.7371	0.8480	0.9840
	M200	15	0	0.7603	0.0399	0.1544	0.4661	0.6097	0.8098	0.8838	0.9299
	Y-15	15	0	0.3756	0.0238	0.0923	0.2501	0.3184	0.3473	0.4109	0.6083
	Y15	15	0	0.7009	0.0294	0.1140	0.5429	0.6342	0.6665	0.7878	0.9440
	Y35	15	0	0.7097	0.0278	0.1075	0.5549	0.6273	0.6695	0.8308	0.8940
	Y70	15	0	0.7156	0.0224	0.0869	0.5989	0.6768	0.6854	0.7278	0.9017
	Y120	15	0	0.7470	0.0219	0.0847	0.6075	0.6924	0.7435	0.7938	0.9057
	Y200	15	0	0.7960	0.0248	0.0961	0.6650	0.7015	0.7810	0.8779	0.9630
MFI species cover											
	O-15	15	0	0.9053	0.0274	0.1062	0.6719	0.8452	0.9513	0.9856	1.0000
	O-35	15	0	0.8996	0.0285	0.1106	0.5538	0.8600	0.9231	0.9822	0.9949
	O15	15	0	0.4243	0.0810	0.3136	0.0252	0.1364	0.3846	0.6374	1.0000
	O35	15	0	0.3496	0.0831	0.3220	0.0079	0.0636	0.2340	0.5417	0.9367
	O70	15	0	0.3574	0.0879	0.3405	0.0000	0.0370	0.2315	0.8083	0.9363
	O120	15	0	0.2468	0.0606	0.2345	0.0161	0.0313	0.1892	0.3723	0.7818
	O200	15	0	0.1945	0.0637	0.2466	0.0000	0.0177	0.1563	0.2560	0.9174

Variable	Treatment	N	N*	Mean	SE Mean	StDev	Minimum	Q1	Median	Q3	Maximum
MFI species cover continued...											
	M-15	15	0	0.9474	0.0262	0.1013	0.6101	0.9274	0.9896	1.0000	1.0000
	M-35	15	0	0.9696	0.0108	0.0416	0.8462	0.9552	0.9843	1.0000	1.0000
	M15	15	0	0.4873	0.0991	0.3839	0.0043	0.0649	0.4481	0.8632	0.9730
	M35	15	0	0.444	0.102	0.397	0.000	0.025	0.503	0.859	0.960
	M70	15	0	0.2870	0.0875	0.3390	0.0000	0.0350	0.1136	0.3654	0.9712
	M120	15	0	0.2592	0.0939	0.3635	0.0000	0.0422	0.0714	0.2400	0.9609
	M200	15	0	0.2120	0.0815	0.3158	0.0000	0.0138	0.0488	0.2308	0.8924
	Y-15	15	0	0.8223	0.0584	0.2261	0.1031	0.7701	0.7571	0.9519	0.9608
	Y-35	15	0	0.7746	0.0430	0.1663	0.4793	0.6000	0.8931	0.9760	0.9892
	Y15	15	0	0.0875	0.0253	0.0978	0.0000	0.0165	0.0759	0.1282	0.3571
	Y35	15	0	0.0594	0.0141	0.0547	0.0000	0.0236	0.0431	0.0885	0.2000
	Y70	15	0	0.0963	0.0202	0.0781	0.0000	0.0196	0.0826	0.1622	0.2727
	Y120	15	0	0.02477	0.00649	0.02513	0.00000	0.00510	0.02174	0.03846	0.08523
	Y200	15	0	0.0273	0.0202	0.0781	0.0000	0.0000	0.0074	0.0147	0.3077
MFI species richness											
	O-35	15	0	12.000	0.676	2.619	7.000	9.000	12.000	13.000	15
	O-15	15	0	11.800	0.380	1.474	10.000	11.000	12.000	14.000	15
	O15	15	0	8.867	0.768	2.973	3.000	7.000	9.000	12.000	14
	O35	15	0	7.60	1.09	4.22	1.00	4.00	8.00	11.00	15
	O70	15	0	6.400	0.975	3.776	0.000	3.000	7.000	10.000	10
	O120	15	0	5.800	0.901	3.489	1.000	3.000	7.000	8.000	13
	O200	15	0	4.600	0.792	3.066	0.000	1.000	5.000	7.000	9
	M-35	15	0	12.067	0.547	2.120	8.000	10.000	13.000	13.000	15
	M-15	15	0	11.733	0.628	2.434	6.000	11.000	12.000	14.000	15
	M15	15	0	7.27	1.24	4.80	1.00	3.00	5.00	11.00	17
	M35	15	0	6.07	1.11	4.32	0.00	2.00	6.00	9.00	13
	M70	15	0	4.467	0.878	3.399	0.000	1.000	4.000	6.000	11
	M120	15	0	5.47	1.12	4.34	0.00	1.00	5.00	10.00	12
	M200	15	0	4.533	0.935	3.623	0.000	1.000	4.000	8.000	11
	Y-35	15	0	10.400	0.349	1.352	8.000	9.000	9.000	10.000	12
	Y-15	15	0	9.200	0.439	1.699	5.000	8.000	10.000	11.000	13
	Y15	15	0	4.133	0.639	2.475	0.000	2.000	4.000	6.000	9
	Y35	15	0	3.400	0.533	2.063	0.000	2.000	3.000	6.000	6
	Y70	15	0	3.800	0.571	2.210	0.000	2.000	4.000	6.000	7
	Y120	15	0	1.933	0.492	1.907	0.000	1.000	1.000	3.000	7
	Y200	15	0	0.733	0.228	0.884	0.000	0.000	1.000	1.000	3

3.2.4 Species richness variation

Table 3-N. Species richness levels by regrowth-age and position

Position:	Mature	Near	Far
Young	14.4 ± 2.7 ac	15.5 ± 3.6 a	12.6 ± 3.8 b
Mid	14.8 ± 3.3 ac	13.8 ± 3.6 abc	14.1 ± 3.9 abc
Late	15.1 ± 2.6 a	16.0 ± 3.8 a	13.7 ± 3.4 bc

Within age class tests for differences in mean richness among position based on paired T-test, between age-classes differences used 2 sample t-test.

Letters in common denote T-Values with an alpha level of significance, $P > 0.05$

Chapter 4 Appendices

4.1 Description of data sets used for Chapter 4 analyses

Plot data was pooled from three sources (Table 4–A). The plot selection process for each project is described in detail below.

Table 4-A. Sampling strategies of all projects from which plots were pooled for analysis

PROJECT/ Stratification variable			Forest age class					
1.Experimental forest landscape (EFL)	**Stratification Classes**	**YSR <10**	**OSR 20-29**	**OSR 30-50**	**MR 70-110**	**OG >110**	**Subtotal**	
/Landscape Context Class (LCC)	**3**	**0**	**0**	**7**	**0**	**0**	**7**	
LCC	**4**	**0**	**0**	**7**	**5**	**2**	**14**	
LCC	**5**	**0**	**1**	**6**	**2**	**5**	**14**	
LCC	**6**	**0**	**2**	**5**	**7**	**0**	**14**	
LCC	**7**	**0**	**0**		**6**	**1**	**7**	
	EFL Subtotal							**56**
2. Wet forest Chronosequence (WCP)								
/Aspect	**South**	**1**	**0**	**2**	**2**	**1**	**6**	
Aspect	**North**	**1**	**0**	**2**	**2**	**1**	**6**	
	WCP Subtotal							**12**
3. Mature Forest Influence (MFI)								
/Forest type	**SR**	**5**	**5**	**4**			**14**	
Forest type	**Mat**				**7**	**8**	**15**	
	MFI Subtotal							**29**
4. Extra plots /Random		**0**	**0**	**2**	**3**	**5**		**10**
Total		**7**	**8**	**35**	**34**	**23**		**107**

Table 4–A Notes

1. Experimental Forest Landscape project (EFL)

The vegetation in 56 EFL plots was surveyed in 2010 to measure response of species to differences in LC influence. For this purpose the study area was stratified according to both LC class and forest types.

The 2009 PI map was used to classify vegetation into ten classes of which only two forest-types were sampled: mature forest and older silvicultural regrowth forest. Mature forest had more than 5% canopy cover of mature eucalypts (>110 years old) and had not been logged or burnt in the past 50 years. Older silvicultural regrowth forest (OSR) had more than 5% canopy cover of regrowth eucalypts between 20 and 50 years old in 2009 and less than 5% cover of mature eucalypts; most had been clear-felled but a couple may only have been subject to selective logging and burnt by 1967 wildfires.

Ten LC classes calculated from the 2009 PI map were mapped at three different spatial scales : 500 m, 1 km, 2 km (Wardlaw et al. 2012). Sampling was restricted to LC classes 3 to 7 and only sites with the same LC class at all three spatial scales were selected. Mature forest was rare in LC class 3 and older silvicultural regeneration was rare in LC class 7 preventing the sampling of these two treatment combinations. Seven replicate plots were located within all other treatment combinations. Plot locations were also constrained to State Forest land areas not being harvested during the sampling period, accessible from roads, and not closer than 50 m from a hard edge (recently harvested coupe, road, major river). The final plot locations within each treatment combination were selected to minimise spatial auto-correlation and confounding between the LC class gradient and the strong east-west climatic gradient. Plot locations were random with respect to substrate and topographic variation.

2. Wet forest chronosequence project (WCP)

Twelve long term wet forest monitoring plots were established to represent single cohort eucalypt forest in a chronosequence of four regeneration age classes: old growth: n=2, 1898–1934: n=4, 1966/67 n=4, 2000s: n=2; and two disturbance types: clear-fell burn and sow silviculture (CBS), or wildfire(WF). Two of the 1966/67 plots and 2000s plots had been clear-felled, but all others were subject only to wildfire disturbance. Replicate age class plots were stratified according to two aspect classes (north/south). Plot locations were restricted to State forest land with Jurassic dolerite or Quaternary substrates and gentle to moderate slopes and arranged to minimise confounding between the climatic gradient and forest age class. They were established as far as possible in areas of relatively uniform forest type dominated mainly by

E. obliqua, 200 m buffer from hard edges. The plots were surveyed between 2007 and 2008.

3. Mature forest influence project (MFI)

Five replicate clear-felled coupes were chosen to represent each of three regeneration age classes (1966–72, 1980s and 2000s). Coupe selection was constrained to those with mature forest edges. Final selection attempted to minimise spatial auto-correlation and confounding between the climatic gradient and coupe-age classes. Within each of these clear-felled coupes a 50 by 50 m plot was randomly located and a matching paired plot was established in the adjoining mature forest patch. One of the selected clear-felled coupes had already been sampled by the EFL project and so was excluded from the pooled data set to avoid duplication of sampled sites. Vegetation of these plots was surveyed in 2011.

4. Extra plots

Some additional plots were surveyed at random in other forest vegetation in 2011 to increase replication, particularly for mature forest. Three of these plots were established more than 2 km from the nearest road and were measured as remote control sites for the EFL project.

4.2 List of environmental predictors

Table 4-B. List of site predictor variables (V) used in Multivariate Analysis (M) Random forest analyses (R1-3) and beta regression modelling (B)

V group	V Name	Variable Definition	M	R1	R2	R3	B
c	TAM	Temperature annual mean in degrees Celsius, average of mean weekly (BIOCLIM parameter 1)	X	X	X	X	X
c	TSE	Temperature seasonality, coefficient of variation of mean weekly temperatures (BIOCLIM parameter 4)	X	X	X	X	X
c	TMX	Mean maximum temperature for the warmest month (BIOCLIM parameter 5)	X	X	X	X	X
c	TMN	Mean minimum temperature of the coolest month (BIOCLIM parameter 6)	X	X	X	X	X
c	PPA	Mean annual precipitation in mm (BIOCLIM parameter 12)	X	X	X	X	X
c	PPD	Mean precipitation of the driest month in mm (BIOCLIM parameter 14)	X	X			X
c	PSE	Precipitation seasonality, coefficient of variation of weekly Rainfall (BIOCLIM parameter 15)	X	X			
c	PPW	Mean precipitation of the warmest quarter (BIOCLIM parameter 16)	X	X	X	X	X
c	RLW	Radiation of the lowest month (BIOCLIM parameter 22)	X	X			X
c	RWM	Radiation potential for the warmest quarter (BIOCLIM parameter 26)	X	X	X	X	X
c	RSP	Radiation estimate for January to March adjusted for aspect and rainfall	X	X			X
c	RDA	Annual radiation estimate adjusted for hill shade and aspect	X	X	X	X	
d	AF3	Age when last disturbed in three classes (Y<50 years, M 50-110, O >110)		X	X	X	X
d	AGE	Age since last disturbance in years	X	X	X	X	X
d	AG2	Age since last disturbance in two classes (<50 yrs, >50 yrs)		X	X		X
d	AG4	Age since last disturbance in four classes (YSR, OSR, MR,OG)		X			
d	AG6	Age since last disturbance in six classes (0–19,20–39,40–59,60–79,80–109,>110)		X			
d	FF2	Disturbance frequency in classes 1=disturbed once or less often in past 110 years; 2=Disturbed twice or more times in the past 110 years)	X	X	X	X	X
s	GO3	Geological substrate in three classes: P=Permian mudstone or derived talus or alluvium; J=Jurassic dolerite or derived talus or alluvium; or T=Tertiary sandstone		X			
s	GO4	Geological substrate in four classes: Permian mudstone (Pm); Quaternary talus or alluvium (Qt); Jurassic dolerite (Jd); Tertiary sandstone (Ts)		X	X	X	
s	ALU	Soil aluminium estimated in mg/l	X	X	X	X	X
s	CAL	Soil calcium estimated in mg/l	X	X	X	X	X
s	CYD	Estimated percentage of clay between 1 m and 2 m of soil based on state-wide soil modelling.	X	X			
s	CYM	Estimated percentage of clay between 30 and 100 cm of soil based on state-wide soil modelling.	X	X			
s	CYT	Estimated percentage of clay in top 30 cm of soil based on state-wide soil modelling.	X	X			X

V group	V Name	Variable Definition	M	R1	R2	R3	B
s	CND	Soil conductivity (top 15 cm of soil tested in solution with distilled water)	X	X	X	X	X
s	POT	Soil potassium estimated in mg/l in three classes (Low: <125; Medium:125–224; High: ≥225)	X	X			X
s	MG3	Soil magnesium estimated in mg/l in three classes: (Low: <150; Medium: 150–249; High: ≥250)	X	X			
s	NIT	Soil nitrogen estimate in mg/l	X	X	X	X	X
s	PHW	Soil pH (top 15 cm of soil tested in solution with distilled water)	X	X	X	X	X
s	SLD	Estimated soil drainage index based on state-wide soil modelling.	X	X			
t	AS4	Aspect in Four classes: North; East; South; West.		X			
t	CAS	Cosine of aspect	X	X		X	
t	CRV	Average curvature	X	X	X	X	
t	FLA	Flow accumulation index	X	X			
t	NNS	Northness Index	X	X			X
t	NWS	Northwestness Index	X	X	X	X	X
t	PNC	Plan curvature	X	X	X	X	X
t	PFC	Profile curvature	X	X	X	X	X
t	SLP	Percentage slope	X	X		X	X
t	TIN	Topographic Position Index	X	X			X
t	TOP	Topographic position in 5 classes (GV: gully/valley flats; SF: lower slope SM: mid-slope, SS: upper slope, HR: ridge or hill top)		X			
e	DOM	Dominant eucalypt at the site (E. regnans or E. obliqua)					X

Notes explaining derivation of variables presented in Table 4–C:

Interpolated climate data were extracted from the 2007 state-wide coverage for 32 BIOCLIM parameters (Nix and Busby 1986) prepared by the Landscape Logic project using the ESOCLIM© module of ANUCLIM© Version 5.2 (Houlder et al. 2000) and a 25 m digital elevation model. Topographic variables were all generated from the 25 m state-wide Digital Elevation Model, calculated from a 3 x 3 grid cell kernel. Topographic position index was calculated as the difference between the elevation of the cell and the mean elevation of all cells in a buffer radius of 200 m (Jenness 2006). Northness index (Holden et al. 2009) was calculated by multiplying the percentage slope by the cosine of the aspect (in degrees). This calculation was adjusted by adding 45 degrees to the aspect to calculate Northwestness. Soil drainage and clay content were extracted from state-wide coverages (Department of Primary Industries, Parks, Water and Environment, unpublished data). All raster data were extracted using bilinear averaging sampling technique in ARC GIS.

Geological substrate for each plot was obtained from the 1:250,000 geological map of Tasmania. Soil data were based on test results for soils sampled from the plots.

Five samples of surface soil to a depth of 10 cm were collected from each of four subplots and air-dried as soon as possible after collection. Soils were ground and sieved using a 2 mm sieve to remove roots, twigs, leaves and stones. Equal volumes of soil from each subplot within a plot were bulked together and tested for nutrients using the standard procedure recommended for the Palintest Soil kit (Palintest Ltd undated). All but one plot had soils tested for pH, conductivity and nitrogen. The plot for which soil was missing (having been logged before soils were collected) was assigned the median recorded pH, conductivity and nitrogen for plots classified into the same vegetation and age class group. Calcium and magnesium were measured in 81 plots including 77 out of the 84 regrowth plots while potassium and aluminium were measured for 71 and 69 plots respectively. Values of soil nutrients were predicted for remaining plots on the basis of pH, conductivity, geological substrate, mean annual temperature, mean annual rainfall, time since last fire and slope using the Random Forests classification method (Breiman 2001). On the basis of the test data set, predictions were accurate to 85% or better for class thresholds. For calcium and aluminium midpoint values of the three and four classes (respectively) were incorporated into the measured data set rather than reducing the precision of the measured data. For magnesium and potassium data were allocated to the three classes for which predictions could be made with confidence for the remaining soils.

4.3 List of landscape context metrics

Table 4-C. Landscape Context metric predictor variables /candidates used in Multivariate Analysis (M), Random Forests analyses (R1-3) and beta regression modelling (B).

Group	LC code	Type	Definition of LC metric	M	R1	R2	R3	B
p	SIZ	Area	Patch size in which the plot is located		X			
v	NFA	Proportion	All non-forest vegetation including plantations, agricultural land, scrub and other non-tree dominated native vegetation		X	X	X	
v	NAP	Proportion	Agricultural land and plantations			X		
v	NNF	Proportion	Native non forest and scrub vegetation			X		
v	SVO	Proportion	Silviculture regrowth only (20 to 50 years of age)			X	X	
v	F20	Proportion	Forest disturbed in the last 20 years		X	X		
v	F40	Proportion	Forest last disturbed between 20 and 40 years ago		X	X		
v	F60	Proportion	Forest last disturbed between 40 and 60 years old		X	X	X	
v	FCX	Proportion	Forest last disturbed between 60 and 110 years old		X	X		X
m	OGR	Proportion	Forest last disturbed more than 110 years ago including rainforest of unknown age		X	X	X	X
m	RNF	Proportion	Rainforest (forest with myrtles and less than 5% mature eucalypt cover)		X	X		X
m	RFM	Proportion	Rainforest and Mature eucalypt forest		X	X		X
m	MED	Proportion	Mature eucalypt forest (forest with more than 5% cover of mature eucalypts)		X	X	X	X
m	MEA	Proportion	All vegetation with mature eucalypt trees (cover > 0%)		X	X	X	X
m	MDN	Density	Average mature eucalypt density		X	X	X	X
m	PMR	Distance	Distance to nearest mature forest (eucalypt forest, rainforest or mixed forest including partially cleared mature eucalypt forests in which mature eucalypts or myrtles were retained)		X		X	X
m	POG	Distance	Distance to nearest old growth forest (eucalypt forest not disturbed for more than 110 years, rainforest or mixed forest, excluding vegetation burnt less than 110 years ago not mapped as having myrtles)		X		X	X
m	PO4	Distance	Distance to nearest old growth forest in four classes: <63; 63–125, 125-250, > 250 m					X
m	PM3	Distance	Distance to nearest mature forest in three classes: <63; 63–125, >125 m					X
m	PM4	Distance	Distance to nearest mature forest in four classes: <63; 63–125, 125–250, > 250 m					X
	PM2	Distance	Average of POG(F), POG(C), PM(F) in two classes: ‘near’ and ‘far’	X				

4.4 Indicator species analysis plot age groupings

Table 4-D. Classes used in Indicator Species Analysis

Number of classes	Class age range (in years)				
Two	< 50			>70	
Three	< 50			70–110	>110
Four	<40		40–49	70–110	>110
Five	<10	20–39	40–49	70–110	>110

4.5 Assemblage response to age and fire frequency classes

Table 4-E. PERMANOVA results for fixed age factor model including eleven covariates

Source	df	SS	MS	Pseudo-F	Estimate of Components of Variation (sq root)
sCAL (covariate)	1	11536	11536	8.65***	11.03
sN20 (covariate)	1	12602	12602	9.45***	10.70
sTIN (covariate)	1	10360	10360	2.11*	9.36
cPPD (covariate)	1	10346	10346	6.87***	9.87
sALU (covariate)	1	8225	8225	6.17***	8.16
cTAM (covariate)	1	5706	5706	4.28***	7.21
tNWS (covariate)	1	5590	5590	4.19**	6.31
cTSE (covariate)	1	3240	3240	2.43*	5.99
sPHW (covariate)	1	3315	3315	2.49**	5.84
sDRA (covariate)	1	2740	2740	2.06*	3.79
dAG4) (fixed factor)	3	19997	6666	5.00***	15.96
dFF2 (fixed factor)	1	26698	26698	20.0***	15.40
Residuals	64	122630	1333		36.51
Total	83	242980			

Unique Perms all ≥9898, *** P ≤0.0001, ** 0.001<p <0.01 * 0.01<p<0.05, n.s. p>0.1

4.6 Relative model strengths for each set of plots

Table 4-F. Median pseudo R-squared for best model^ (of 5 variable sets tested) by plot set

Plot set	Number of spp*	Median p-R^2 *	Friedman's Estimated Median p-R^2 (n=26 species) #	Friedman's Sum of Ranks
All	55	0.32 a	0.33	96
All silviculture ages	53	0.33 a	0.32	91
OSR	50	0.35 a	0.35	108
All mature tree	50	0.34 ab	0.35	107
MR	53	0.35 a	0.36	107
OG	39	0.44 bc	0.39	126
All regrowth	54	0.32 a	0.32	96
Grand Median			0.34	

^ The same five candidate sets (SFF, SCY, S, CY, and FF) were used to select the best model for this analysis;

Species with best model p-$R^2 \geq 0.1$

Friedman's test among same species (n = 26) $P = 0.34$ (adjusted for ties), df = 6

4.7 Variable group importance for predicting species abundance in older silvicultural regrowth forest

Table 4-G. Random Forest models of abundance for 42 species within older silvicultural regrowth forest. (See notes at end of table)

	1.R2 $	2. Mature metrics (R2)			3. Other (R2)	4. Site Variables (R2)				5. Best RF model #			
Species name	p-R^2	+/-	IV	Code	V	C	S	D	T	Mod	p-R^2	LCrl	IVMA
+ve LC association													
Nothofagus cunninghamii	64	+	33	MOG nC						CS	70	16	+20
Anodopetalum biglandulosa	37	+	20	POG F		+13 PPW				CS	53	39	+30
Eucryphia lucida	29	+	16	MEA nC		+17 PPW				CS	44	10	+28
Dicksonia antarctica	32	+	18	MEA nC		+13 TAM				All	32	67	+18
Anopterus glandulosa	17	+	10	POG F		+11 TSE				CS	35	13	+12
Gahnia grandis	26	+	11	MDN fC	-17 F60 nC	+09 TMN		-11 AGE		SS	48	0	0
Atherosperma moschatum	11	+	12	OGR fC		+09 PPW	+13 CND			F	28	71	+22
Lepidosperma ensiforme	28	+	24	POG F			+15 PHW			All	28	81	+24
Acacia dealbata	50	+	05	PMR C			+35 NIT		-08 PNC	CS	51	02	0
Hymenophyllum peltata	26	+	14	OGR nF			+16 ALU	+16 AGE	+12 CRV	FS	28	0	11
Trochocarpa gunnii	23	+	08	POG F	-11 F40 fF		-06 ALU			SLn	42	0	0
Leptecophylla juniperina	39				-13 F60 fC		-13 GO4	-18 AF3		SLa	52	07	+11
Tmesipteris obliqua	29	+	20	MED nC				13 AF3		SLa	40	68	+31
Eucalyptus delegatensis	19	+	14	OGR fC					+03 PFC	C	48	88	+16
Eucalyptus regnans	31				-36 NFA nF					All	31	61	0
-ve LC association													
Dianella tasmanica	31	-	11	MDN fF	+15 NFA fC	+09 PPW				S	57	0	0
Cyathodes glauca	33				+18 F60 nC	+21 RDA				FS	39	15	+18
Zieria arborescens	38	-	9	PMR C	+16 NFA nF	+11 TMX			+13 CAS	FS	39	05	0
Clematis aristata $$	33				+09 SVO nC	+25 TAM	+06 PHW		+05 SLP	SLa	39	01	+10

Species name	1.R2 $ p-R^2	2. Mature metrics (R2) +/-	IV	Code	3. Other (R2) V	4. Site Variables (R2) C	S	D	T	5. Best RF model # Mod	p-R^2	LCrl	IVMA
Nematolepis squamea	28	-	18	MDN fF		+16 TAM	-18 CND			CS	43	03	-13
Leptospermum scoparium	27	-	0.1	PMR F		+04 TMN	-22 CAL			SLa	34	01	0
Melaleuca squarrosa					[+NNF aF]	[-PPW]	[-18 PHW]			SLa	28	0	0
Monotoca glauca	61	-	13	PMR F	+17 NFA fF		-31 PHW			SLa	66	06	0
Eucalyptus obliqua	34	-	10	OGR fF			-28 NIT			All	34	14	-10
Drymophila cyanocarpa	34	-	23	MED nF			-38 CAL			SLn	47	23	-28
No LC association													
Pomaderris apetala	61					+17 TAM	+29 CAL			FS	61	01	0
Pimelea cinerea	39					+23 PPW		+18 AF3		All	39	01	0
Correa lawrenceana	20					-13 PPW			+14 CAS	CS	35	21	0
+/- LC association													
Hymenophyllum flabellatum	34	+	11	OGR nF	-/+13 F60 nC			+16 FF2		FS	42	11	+15
Hymenophyllum cupressiforme	37	+	23	OGR nF	+35 NFA fC			+28 AGE		All	37	76	+28
Hymenophyllum australe	39	+	14	MEA fF	+13 F60 nC	+17 TSE		+13 AGE		FS	44	08	+17
Hypolepis rugosula	33	+	15	OGR nF	+08 F60 fF	+16 TAM				FS	53	10	-17
Blechnum wattsii	18	+	12	MEA fF	+08 SVO nF	+08 RDA				All	18	100	+12
Grammitis billardierei	41	+	16	PMR C	+24 F60 nC		+18 PHW	+25 AGE		FS	43	12	+15
Olearia argophylla	11	+/-	11	MED nC			+09 CND	+10 AGE		CS	43	79	+31
Hymenophyllum rarum	25				+/-14 F60 fF		+10 CND	+09 AGE		FS	41	18	+13
Rumohra adiantiformis	21	+/-	14	PMR F	+09 NFA fF		+17 CND			FS	32	08	0
Ctenopteris heterophylla	39	+/-	19	MED nC			+20 CND			SLn	40	43	+17
Pimelea drupacea	26	-	13	MED fF	-15 F60 nC	+17 TAM	+11 CAL		+12 SLP	SLa	34	01	0
Pittosporum bicolor	11	-/+	7	OGR fF	-/+12 SVO nC				-13 PNC	FS	30	45	+13
Histiopteris incisa	20	-/+	17	MED fC	+16 SVO nC					All	20	98	+17

Notes explaining data presented in Table 4–G:

Only species for which the p-R^2 was > 0.26 for the best model are included (n = 43, p-R^2 > 0.26, P < 0.1).

$$ *Clematis aristata sensu lato* (Curtis and Morris 1975)

Column sections 1 to 4 provide a summary of results from models produced from a single set of predictors (R2 see Table 4–C and 4–D for the complete list, for more details refer to the methods section)

Section 1: $R2^{\$}$ = pseudo-R^2 result for each species based on the same set of 47 candidates including both site variables and LC metrics (following fire and current year landscapes calculated for 500 m and 1000 m scales).

Section 2: The species association (+ /-) with mature forest metrics: positive indicates increasing abundance within increasing amount of mature forest or with greater proximity to mature forest; followed by the Importance Value (IV, Gini index) and code for the highest ranking mature forest metric which was selected as one of the six most highly ranking predictors of species abundance in the model, the code for the mature forest metric (see Table 4-D for explanation of codes) is followed by the spatial scale (n = 500 m, f = far) and the temporal scale (F = landscape following the fire year; C = 2009 landscape) at which the metric selected was calculated. Table 4–H provides further information about the importance value of all mature forest metrics selected of the top six ranking predictors.

Section 3: The species association (+ /-) with other vegetation metrics: positive indicates an increasing abundance in association with increasing amounts of non-forest and young regrowth forests in the landscape; followed by IV and code for the highest ranked metric (For more detail see notes for columns in section 2, metric codes are explained in Table 4–D).

Section 4: Data for highest ranking site variables from each of four variable groups that were included in species model listing the species association with the group first followed by the IV and code (explained in Table 4–C), a positive association was listed for:

C = **climate variables:** if species abundance increased with rainfall and declined with temperature and radiance;

S = **soil variables:** if species abundance increased with pH, Calcium, Nitrogen or Conductivity but declined in with increases in Aluminium;

D = **disturbance variables:** if species increased in association with forest age, or age when last disturbed but decreased with increased fire frequency

T = **topographic variables:** when species abundance increased with slope or increased with more northerly aspects, and increased convexity in plan, profile and average curvature (ridges, upper slopes, crests).

Column section 5 provides the summary of information from the best models produced from all candidate sets tested (R1, R2, R2 in Table 4–C and 4–D, for more details refer to the methods section) Codes defining the predictor sets:

All = full set of metrics and variables;

C = CY metrics only;

CS = CY metrics and site variables;

FS = FF metrics and site variables;

SS: full set of site variables only;

S = Subset of Site variables only;

Sla = Site and FF and CY metrics LC at 250 m scale;

Sln = Site and FF and CY metrics LC at 500 m scale.

Summary of results for best Random Forest models

Out of 39 species for which robust models were produced using Random Forests from older silvicultural forest plots (p-R^2 > 0.26, n = 43), only two species (*Gahnia grandis* and *Dianella tasmanica*) had best models developed from candidate sets without any LC metrics while two had equal best models produced from candidate sets with LC metrics but no LC metrics were included among the top six variables (*Melaleuca squarrosa, Trochocarpa gunnii*). The best models for another five species included LC metrics in the candidate sets but none among the top six most highly ranked. Of the nine species for which LC metrics were relatively unimportant, none were indicators of older forest classes and *Trochocarpa gunnii* was the only shade-tolerant

rainforest species among them. The others were either indicators of silvicultural regrowth (*Acacia dealbata, Gahnia grandis, Pimelea cinerea, Pomaderris apetala)* or not indicators of any particular forest age-class *(Correa lawrenceana, Dianella tasmanica, Leptospermum scoparium, Melaleuca squarrosa, Trochocarpa gunnii).*

Of the thirty species for which LC metrics were important, twenty-four included at least one mature forest metric among the most important explanatory variables of which six included both mature forest and other vegetation metrics. Eighteen included only positive associations with mature forest metrics, two included both positive and negative associations (*Olearia argophylla,* and *Cyathodes glauca*) and four included only negative associations (*E. obliqua, Drymophila cyanocarpa, Leptospermum scoparium* and *Nematolepis squamea).* The only silvicultural regrowth indicator among those with positive associations with mature forest metrics was *Leptecophylla juniperina*. There were no older forest indicators among species with only negative associations with mature forest metrics. Of the sixteen species including positive associations with mature forest metrics five included negative associations with other vegetation metrics also. *E. regnans* and *E. obliqua* were the only other species to be negatively associated with other vegetation metrics (Table 4–G).

4.8 Temporal and spatial scale of mature forest metrics selecting in Random Forest models of species abundance in older silvicultural

Table 4-H. Summary of the mature forest metrics selected in Random Forest models to predict abundance of 31 species in older silvicultural regrowth

The sign of association (+ /-) and Importance Value (IV, Gini Index) are listed for the highest ranking variable in each metric type[#]. For other details about model results for these species refer to Table 4–G in Appendix 4.7.

Species	Model	Landscape Year selected		Scale or Distance metric selected			Metric Forest	Plant traits			
	p-R^2	Fire	Current	500 m	1000 m	Proximity	Type	Pm	Dm	LF	Ind
Lepidosperma ensiforme	28	+24				+24	M	s	i	h	s
Blechnum wattsii	18	+12			+12		M	r		f	o
Hymenophyllum australe	39	+14		+13	+14		M			f	o
Hymenophyllum cupressiforme	37	+23		+23			O			f	
Hymenophyllum peltata	26	+14		+14			O			f	o
Hymenophyllum flabellatum	34	+11		+11			O			f	r
Hypolepis rugosula	33	+15	+09	+15			O			f	s
Trochocarpa gunnii	23	+08	+06	+06		+08	O		i	w	
Anopterus glandulosa	17	+10	+06	+06		+10	O	r	w	w	o
Anodopetalum biglandulosa	37	+20	+17		+13	+20	O	r		w	o
Eucalyptus delegatensis	19	+07	+14	+14	+14		O	rc		w	s
Dicksonia antarctica	32	+16	+18	+18	+16		M	r		f	r
Atherosperma moschatum	11	+10	+12	+10	+12		O	r	p	w	o
Nothofagus cunninghamii	64		+33	+33			O	r		w	o
Tmesipteris obliqua	29		+20	+20	+19		M			f	o
Eucryphia lucida	29		+16	+16	+14		M	r		w	o

Gahnia grandis	26		+11	+09	+11		M	s	i	h	s
Grammitis billardierei	41		+16			+16	M			f	o
Acacia dealbata	50		+05			+05	M	s	w	w	s
Zieria arborescens	38		-09			-09	M	s		w	s
Monotoca glauca	61	-13	-11	-12		-13	M	s	i	w	s
Eucalyptus obliqua	34	-10	-09		-10	-09	O	rc		w	s
Pimelea drupacea	26	-13			-13		M		i	w	s
Nematolepis squamea	28	-18			-18		M	s		w	
Rumohra adiantiformis	21	+14	-11		-11	+14	M			f	o
Histiopteris incisa	20	+13	+17	+15	-17	-/+15	O			f	s
Olearia argophylla	11	+10	+/-11	+11	-08	+10	M	r	p	w	r
Drymophila cyanocarpa	34	-23		-23	-21		M		i	h	
Dianella tasmanica	31	-11			11	-10	M		i	h	
Pittosporum bicolor	11	-07	+07		-07	+07	O	r	i	w	m
Ctenopteris heterophylla	39		+/-19	+/-19			M			f	r

Positive or negative relationships to a metric are indicated where species abundance increased or decreased in association with all metrics selected from that metric category.

+/- was assigned if more than one metric was selected and the relationship of species abundance with these metrics was inconsistent.

Metric Forest Type codes: O: metrics calculating the proportion or distance to old growth forests, including rainforest, M: metrics calculating the proportion or distance to any mature forest including old growth as well as regrowth forest (> 50 years) with mature eucalypt trees.

Codes for plant traits are listed in the notes for Table 4–3 in Part A Section 4.3.1.

4.9 Species abundance models for all regrowth ages

Only species for which the pR^2 were ≥ to 18 in either Beta-regression or Random Forest model are listed (n = 84, p-R^2 > 0.18, $P < 0.05$).

Data provided for Beta-Regression models include the AIC and pseudo R^2 for the full model together with the relative contribution of the LC metrics to the model (LCbII). The coefficient and standard error for each predictor term is listed within the relevant variable group column followed by the code for the predictor (See Appendix 4.2 and 4.3). Bold indicates the factor level for which the coefficient is listed. Variable fitted in the precision model have an asterisk following the variable code. In addition to the direction of slope provided for each fitted variable, if the association of the species abundance with the variable group as a whole is different to the slope for the fitted variable an additional (+) or (-) is listed prior to the coefficient as per the following table:

Column Code	**Variable Metric group**	**+ indicates species abundance increases with:**
M	Mature forest	increasing amount of mature forest in surrounding area, reducing distance from mature forest
V	Other vegetation	increasing amounts of non- forest and regrowth forest in surrounding area
C	Climatic	increasing with rainfall, cooling temperatures reducing radiation
S	Edaphic	increasing: calcium, nitrogen, potassium, conductivity reducing: aluminium, reducing pH, reducing clay, reducing drainage
D	Disturbance	increasing: age, increased age when last burnt reducing Fire frequency
T	Topographic	increasing: slope, northerliness, convexity, curvature, ridge & crests

For Random Forest models the importance value (gini index) of the highest ranking variable/metric in each of the six variable and metric groups (see table above) is listed together with the metric or variable code which was most important. To demonstrate which the species were positively or negatively associated with variable groups as a whole (grouped by column) '+' or '-' is indicated prior to importance value as per table above. Additional notes are listed below Table 4–I.

Rationale for species groupings:

1. Results agree for both methods: Species positively associated with mature forest metrics
2. Results differ between methods: Only Random Forest models improved with mature forest metrics and species abundance was positively associated with these metrics
3. Results agree: Species negatively associated with mature forest metrics or positively associated with younger forest metrics (Random Forests)
4. Results differ: Beta Regression models not improved with mature forest metrics
5. Results agree: Species abundance not associated with mature forest metrics
6. Random Forests modelling successful with positive associations with mature forest metrics, but no model successful within beta-regression
7. Random Forests modelling successful with ambiguous, negative or no associations with mature forest metrics but modelling unsuccessful in beta regression

Table 4-I. Importance of variables within the best robust models of species abundance in regrowth forest

	Beta Regression Model								Best Random Forests Model							
Species name	AIC	pR2	LCbI	Intercept	Mat	D	C	S	T & (other)	Model	p-R2	LCrI	M	V	D	C	S	T
Species Group 1																		
Cenarrhenes nitida	-1361	17	29	-20.19 ±1.483	+0.0017 ±0.0002 POG F*		+0.0091 ±0.0011 PPA*											
Eucalyptus delegatensis	-1352	18	36	-3.1645 ±0.7748	+10.906 ±0.945 OGR nF*		(+)-0.476 ±1.046 TMN*		-5.396 ±1.054 NNS*	SLr	36	42	+14 OGR rC	-11 NFA rC	-7 AGE	+14 TMX		
Anodopetalum biglandulosum	-1157	19	59	-26.4562 ±1.991	(+)-3.737 ±0.460 PM**3***		+1.175 ±0.108 PPD*	-0.789 ±0.314 POT**4**		SLf	43	100	38 RNF fC			+31 PPW		
Melaleuca squarrosa	-1376	21	20	-17.1999 ±2.3444	+ 4.77 ±0.79 MED nC*		(-)+0.22 ±0.02 TAM*	-2.51±0.30 PHW* -0.021±0.002 ALU*		CS	33	5	+19 MED aC			-14 TMN	-15 POT	
Anopterus glandulosus	-1036	16	58	0.9451 ±2.5527	+4.19 ± 1.74 mRNF nF C* +0.0009 ±0.0004 POG C		(+)-0.028 ±0.013 TMX	-0.25 ±0.07 NIT*		C	42	100	34 OGR rC					
Acacia verticillata	-1105	20	19	-6.1352 ±1.8235	(+)+4.66 ±1.68 MCX nF*		(-)+ 0.038 ±0.017 TAM	- 0.041 ±0.007 CND*		SF	28	59	21 FCX rF			-14 TMX	-16 CND	
Phyllocladus aspleniifolius	-948	43	77	-4.5354 ±0.7229	+7.71 ±1.41 RNF nF*		(+)-0.493 ±0.120 TMN*	-0.0044 ±0.0015 ALU		F	36	100	19 MRF aF	18 F40 fF				

Group 1 cont.																			
Tmesipteris obliqua	-1326	31	26	1.6721 ±2.1192	(+) -2.057 ±0.312 PM**3***		+0.252 ±0.055 RLW*	0.202 ±0.044 +NIT*	-0.168 ±0.020 TIN*	SMn	30	08	14 MED nC			14 RLW	22 NIT	
Polystichum proliferum	-994	11	74	-7.7546 ±0.4032	+0.081 ±0.166 MDN nF*			+0.0013 ±0.0003 CAL		SLa	25	38	17 RFM aC					21 PFC
Drymophila cyanocarpa	-1173	18	02	-4.8927 ±0.4733	+1.954 ±0.896 MED nC*			-0.028 ±0.004 CND*	-2.407 ±0.372 DOM**r***	CS	28	25	28 RFM fC			-23 PPW	-23 CYM	
Blechnum wattsii	-805	21	07	-6.4246 ±0.4309	+3.54 ±0.92 MED nC*	(+)-0.50 ±0.22 FF**2**		+0.010 ±0.003 CND		C	12	100	23 MDN aC					
Nothofagus cunninghamii	-736	59	05	2.5624 ±2.7468	+0.70 ±0.34 PM**5** F*	(+)-0.628 ±0.237 FF**2**	(+)-0.028 ±0.014 TMX	-0.005 ±0.002 ALU	-3.12±1.36 NWS 0.50±0.24 DOMr	FS	40	0	16 MEA rF		+14 AGE	15 RLW	-21 ALU	
Dicksonia antarctica	-540	33	14	-1.8742 ±1.645	+2.404 ±0.665 MEA nC*	+0.013 ±0.004 AGE*	-0.021 ±0.007 PPW*	+0.167 ±0.027 NIT	+0.011 ±0.003 CND	SMn	31	05	15 PMR F		+20 AG4		31 NIT	
Hymenophyllum australe	-1406	26	14	-13.52 ±0.6993	+13.52±0.70 RNF nC -7.78±1.10 OG nC*	(+)-1.42 0.29 FF**2***	0.130 ±0.019 CYT*	+0.462 ±0.060 NIT*	1.3E-04 2.7E-05 FLA	CS	33	03	+20 RNF fC		+11 FF2		+17 NIT	-17 FLA
Hymenophyllum flabellatum	-1171	33	50	-9.4045 ±1.4705	+5.504±1.125 OGR nF* +4.646±0.682 MEA nC* -0.195±0.0364 MDN nC	+0.072 ±0.006 AGE*	-0.020 ±0.006 PPW*	+0.014 ±0.002 CND		FS	46	14	23 OGR rF	-18 NFA rF	+29 AGE			
Acacia dealbata	-784	44	04	-6.0716 ±0.3848	(+)3.882 ±1.732 MRNF nF	(-)+0.215±0.215 AG**2s** (-)+0.831±0.213 FF**2**		+0.167±0.0277 NIT +0.0005±0.0003 CAL		FS	31	10	+/-21 FCX fF				18 NIT	+17 CRV

Species Group 2																				
Pittosporum bicolor^	**-1063**	23	**04**	452.696 ±64.0406	(+)1.854 ±0.784 MED nF*		-0.053±0.007 PPA* -20.683±2.905 RWM*			SLr	37	19		38 SVO rF	*[-33 TSE]				
Tasmannia lanceolata	**-1054**	40	**26**	0.9943 ±1.8132	(+)1.451 ±0.487 MED nC		(+)-0.074 ±0.017 TAM	+0.008±0.003 CND -0.030±0.013 CYT		SLf	22	02		41 F40 fF					
Pomaderris apetala	**-618**	42	**12**	-3.3581 ±0.7357	(+)3.475 ±0.949 FCX			+0.025±0.004 CAL -0.036±0.14 CYT	3.273 ±1.465 NWS	FS	56	01					49 CAL		
Grammitis billardierei	**-969**	42	**09**	1.2266 ±4.1639	(+)0.777 ±0.257 RFM nF	+0.019 ±0.003 AGE	(+)-0.80 ±0.003 TSE	(+)-0.004 ±0.001 ALU		SMn	50	02	+18 PMR C		32 AGE	29 TSE	26 CND		
Gahnia grandis	**-472**	36	**18**	6.4559 ±1.858	+0.008 ±0.0002 POG C*	-0.030 ±0.005 AGE	(+)-0.043 ±0.016 TAM	-0.109±0.035 NIT -1.415±0.453 POT**3***	-0.652 ±0.243 SLD*	SMn	52	06			-25 AGE	12 TAM	-9 SLD		
Hymenophyllum peltatum	**-1021**	37	**05**	-0.5523 ±2.0286	(+)0.7329 ±0.356 MEA nF	+0.012 ±0.004 AGE	(+)-0.056 ±0.015 TAM -0.0021 ±0.0007 PPA	+0.001 ±0.002 CAL		CS	32	0			25 AGE	15 TAM			
Atherosperma moschatum	**-756**	37	**06**	-2.1711 ±0.2881	(+)-0.686 ±0.286 PO4(**3**)	+2.19 ±0.40 AG2*			-4.33 ±1.40 NWS	S	53	0			24 AG6		12 CYT	16 TIN	

Species Group 3.																		
Senecio minimus	**-1432**	17	**59**	-7.6842 ±0.4865	(-)-0.0012 ±0.0003 PM**RF*** -1.581 ±0.418	-0.040 ±0.004 AGE*		(+)-0.0038 ±0.0015 ALU*	0.067 ±0.013 SLP*	SLr	49	37	-12 RFM rF	-/+16 F40 rC	-27 AGE			
Dianella tasmanica	**-1487**	25	**50**	-6.2817 ±0.6251	(-)0.001 ±0.003 POG F*	-0.953±0.200 AG**2*** (+)-2.483±0.390 AF3**OG** **		-0.017 ±0.002 CND		SLf	36	14	-7 MDN fF	+16 NNF fC	-15 ALF	*[-18 PPA]		1 CRV
Zieria arborescens	**-1235**	29	**77**	-34.3922 ±3.7174	+4.618±1.157 MED nC* -15.811±1.559 OGR nC	-0.036 ±0.008 AGE*	(-)+1.719 ±0.218 RSP*			FS	35	14	*[-9 RFM nC]	+16 NFA nF		-21 TMX	11 PHW	
Pimelea cinerea	**-1381**	22	**43**	-13.8755 ±1.4466	-4.492 ±0.419 MRF NF*		(+)-0.204 ±0.038 TMN*	+2.840 ±0.375 PHW	-0.0033 ±0.0005 CAL*	CS	16	78	-29 MEA nC	-33 NFA rC				
Pteridium esculentum	**-783**	15	**03**	-13.9772 ±3.1454	(-)+0.647 ±0.248 PM**3**		(-)+0.111 ±0.031 TAM*	-0.030 ±0.007 CND * (-)+0.010±0.003 ALU*		FS	39	13	-17 MDN fF			-14 TSE		
Species Group 4.																		
Aristotelia peduncularis	**-1278**	22	**0**	16.8579 ±3.6118		+0.031±0.007 AGE* (+)-2.466±0.493 AF3**<50** *	(+)-1.519 ±0.206 RSP*			SLr	17	12	+13 RNF rC	+14 SVO fR		+12 TSE		
Ctenopteris heterophylla	**-1147**	15	**0**	-4.001 ±2.466	-1.972 ±0.397 MRF nF	+0.062 ±0.006 AGE*	(+)-0.085 ±0.024 TAM	+0.044±0.007 CND* -0.0018±0.0003 CAL*		SMn	20	0	+13 MDN nC		+20 AGE	+18 TSE	+16 CYD	
Rumohra adiantiformis	**-1071**	22	**0**	-7.0597 ±0.2789				+0.705 ±0.281 POT.**H**	+0.612 ±0.372 DOM**r**	SLr	20	85	-18 MDN rC				+22 CND	

Monotoca glauca	**-609**	28		1.1505 ±0.9661		-0.868 ±0.259 AF3**og**	-0.131±0.036 NIT -0.609±0.209 PHW		-0.042 ±0.017 SLP*	FS	54	07	-22 MDN rF				-37 PHW		
Species Group 5.																			
Eucalyptus regnans	**-656**	23	**0**	-137.5 ±44.41	(-) +7.09 ±2.105 RWM*	+0.013 0.005 +/-TAM*	(+)-0.159 0.034 PPA	+0.190 ±0.033 NIT	-1.339 ±0.570 PNC										
Eucryphia lucida	**-1027**	35	**0**	-14.634 ±1.7846		(+)-3.157 ±0.441 FF2*	+0.007 ±0.001 PPA*			SMn	33	08			+38 FF2	+35 PPA			
Olearia argophylla MFI	**-756**	36	**0**	-5.6003 ±0.5164		+0.030 ±0.007 AGE			0.989 ±0.237 DOM**r**	FS	34	21	*[12]	-20 F20 fF	+24 AGE	*[+6 TSE]	+21 NIT		
Eucalyptus obliqua	**-259**	44	**0**	-1.2922 ±0.2098		--0.114 ±0.279 AF**3***		-0.230 ±0.036 NIT	-1.000±0.275 CAS +1.717±0.511 PNC +8.059±2.585 NWS	FS	35	03				-25 TMX	-41 NIT	-15 CAS	
Hymenophyllum rarum	**-1016**	42	**0**	-7.7336 ±0.4165		+0.013±0.003 AGE -0.382±0.184 FF**2**		+0.0009 ±0.0002 CAL*		SLr	42	04	*[+10 MDNnF]	-17 F60 rF	+28 AGE		28 NIT		
Nematolepis squamea	**-666**	25	**0**	-0.4902 ±0.9914				-0.451±0.207 PHW* -0.086±0.036 NIT		SMn	41	05				-24 TAM	-26 CND		
Species Group 6.																			
Asplenium appendiculatum				-12.38 ±0.1528						SLf	18	28	+20 MDN fF			+26 PPW			
Billardiera longiflora				-8.9868 ±0.4584						SLf	66	6	+18 RNF fF		-26 AGE		*[-14 SLD]		

Pimelea drupacea		-6.749 ±0.283		SLf	25	22	+14 MED fF	-21 NFA fC			+13 CAL	+26 NWS		
Species Group 7.														
Blechnum nudum		-8.1397 ±0.3516		F	56	54	-/+39 RNF rF			*[+16 TMX]		*[-10 FLA]		
Acacia melanoxylon				SLr	28	79	+17 RNF rC	+27 SVO				+13 PNC		
Hymenophyllum cupressiforme		-30.35 ±2.635		FS	23	32	+22 PMR	+22 F40 fF	25 AGE					
Leptecophylla juniperina		-13.2579		C	34	65	-/+21 MDN fC	+5 F40 rC						
Clematis aristata		-9.0616 ±0.9454		FS	26	8		+21 F20 aF		24 TAM				
Coprosma nitida		-7.629 ±0.7		SLr	25	28		-24 NFA rC			18 CND			
Trochocarpa cunninghamii		-372.0161 ±60.704		SMn	23	0				18 PPA	-6 CYD	-12 SLP		

Notes for Table 4–I

All regrowth aged plots used in data analyses (i.e. 4–105 years since regeneration); refer to Part B Section 3.1 for details of model development process.

The best Random Forests model (i.e. highest pseudo-R^2) from among results for all candidate sets trialled are reported here. All species were trialled with the same candidate sets. The R2 analyses including near Mature forest metrics for both current and following fire years together with a subset of site variables (R2) is listed here as SMn.

Underlined variables: Where the variable groups were selected in both the R2 analysis and the best model it is underlined. The lack of any line means that no successful model was produced with that particular candidate set for the species.
***[*]**: Where models from the R2 analysis included a variable but it was not included in the best model, the importance value and variable code are included in square brackets.

Variables not bracketed or underlined: Variables not underlined or enclosed in square brackets were not selected in the R2 model, either because of differences in modelling results, or because the modelling was unsuccessful (nothing bracketed or underlined) or because the variable was not included in the candidate set for R2 e.g. 'Other vegetation').

4.10 Landscape context metrics and site variables associated most with individual species abundance in mature forest

Table 4-J. Model strength and most important predictors of individual species abundance within mature forest.

The pseudo-$R^{2,}$ p-R^2 for best model including both LC metrics and site variables [p-R^2 in square brackets are for models developed from site variable only, bold font is used where this was the strongest model] followed by the highest ranking Mature Forest metric (MF); Other Vegetation metric (OV) and Site variables (Site) listing either positive (+) or negative (-) association with that metric/variable and the m Importance Value (GINI index). Results are only for models scoring a p-R^2 >15 (R = 0.38, n = 23, $P < 0.068$) and were the best model from either of two candidate sets: LC metrics from Current Year landscapes & Site variables OR LC metrics from landscapes Following Fire year & Site variables. Site variables listed in square brackets were the highest ranking variable from models derived from site variable only candidate sets, when this model had a higher p-R2 than those with LC metrics, and the highest ranking variable was different. Code abbreviations are explained in Appendix 4.2 and Appendix 4.3.

Table 4-J	all mature plots > 70 years old (n = 57)				Plots 70-109 years old (n = 34)				Old growth plots (n = 23)			
Species name	**pR²**	**MF**	**OV**	**Site**	**pR²**	**MF**	**OV**	**Site**	**pR²**	**MF**	**OV**	**Site**
+MF metrics and/or -OV metrics												
Anopterus glandulosus	31 [19]	+OGR aC(19)	-NFA fC (22)	-dFF3 (18)					48 [36]	+MEA aF (7)	-NFA fF (12)	+CYM (21)
Asplenium appendiculatum	19 [16]		-F40 fC (13)	-tTIN (25)	28 [25]			+sNIT (22)				
Blechnum nudum	41 **[59]**		- F40 rC (12)	+cTMX (16)	46 [25]		-F40 rC (12)	+cTMX (16)				
Blechnum wattsii					26	+ RFM aC (21)			41			-cRSP (19)
Coprosma nitida					17	+MEA fF (16)	-NFA rF (20)					
Crepidomanes venosum	41 [33]		- F40 rF (16)	+sNIT (23)	27 [24]			-TIN (17)				
Drymophila cyanocarpa	38 [35]	+RNF nF (9)	-F40 rF (10)	-gGO4 (24)	42 [39]	+RNF fC (11)		-gGO4 (20)	39 [26]		-NFA nF (18)	+CRV (26)

Table 4-J	all mature plots > 70 years old (n = 57)				Plots 70-109 years old (n = 34)				Old growth plots (n = 23)			
Species name	**pR²**	**MF**	**OV**	**Site**	**pR²**	**MF**	**OV**	**Site**	**pR²**	**MF**	**OV**	**Site**
Eucryphia lucida	60 [39]	+OGF nF (22)	-F40 fF (18)		32	+MEA aF (14)		+cPPD (13)	55 [17]	+MDN nC (25)	-NFA fC (26)	
Gaultheria hispida	28 [22]		-F20 aC (14)	-cTMN (16)	22 [20]	+MED aC (8)		-cTMX (11)	17 **[21]**	+RFM fF (6)		-cTMN (13)
Hymenophyllum australe	41 [36]	-POG F (22)		+sPHW (22)	45 [42]			-gGO3 (28)				
Hymenophyllum flabellatum	44 [23]		-NFA rF (21)	+cRWM (18)	39 [23]	+OGR rC (27)		+cPSE (12)	46 [37]	+RNF nF (15)	-NFA rF (16)	+sNIT (18)
Nothofagus cunninghamii	26 [19]	+RNF aF (19)		-tTIN (19)	25			-sPHW (9)	26 [18]	+RNF fF (14)		+sALU (14)
Orites diversifolia	16	+ RNF fF (8)	-F20 nF (9)	-cTMX (9)								
Phyllocladus aspleniifolius					36	+RFM rC (20)						
Polystichum proliferum	42 [26]	+MED aF (13)		+sNIT (19)	56 [32]	+RNF rF (32)		-tAS4 (31)				
Trochocarpa cunninghamii	61 [51]			-cRLW (43)	27	+OGR fF (12)			50 [33]		+F20 rC (15)	-cRLW (12)
+OV metrics and/or -MF metrics												
Acacia dealbata	28 [22]	-MEA fF (22)		+gGO3 (18)	24 [17]	-MEA fF (10)		+sPOT (9)				
Aristotelia peduncularis	22 [17]	-RNF rC (18)		-cTMX (18)					50	-MEA fC (16)	+F20 fC (9)	-cTSE (8)
Microsorum pustulatum	39 [39]		+ F40 rC (55)		19 [15]	-MDN rF (9)		-tPNC (12)	39 [31]		+ F60 nC (33)	
Pimelea drupacea	19 [21]	-MED aF (13)		+tNWS (22)	32		+FCX nC (13)	-tAS4 (18)	44 [42]			+sPHW (20)
Pittosporum bicolor	25 [19]	-MDN rF (12)	+F20 rF (15)	-cTAM (10)	21 **[35]**		F20 rF (19)	-cTMX (17)				
Pomaderris apetala	35 **[36]**	+POG F (31)		+sCAL (31)	**[19]**			**[+sCAL (18)]**	41 [36]	-RNF rC (17)		+tCAS (21)
Zieria arborescens	52 [32]		+ F20 rF (25)	+cTSE (23)	57 [56]		+ F20 rF (20)	+cTSE (21)				

Table 4-J	all mature plots > 70 years old (n = 57)				Plots 70-109 years old (n = 34)				Old growth plots (n = 23)			
Species name	**pR^2**	**MF**	**OV**	**Site**	**pR^2**	**MF**	**OV**	**Site**	**pR^2**	**MF**	**OV**	**Site**
- MF metrics and -OV metrics												
Coprosma quadrifida	34	+POG F (17)	-F20 rF (16)	+dFF2 (18)	21	-MDN nF (10)	-NFA fF (16)		57 **[58]**	-MEA fF (11)		-sCYT (17)
Olearia argophylla	40 [35]		- F20 rF (20)	+sNIT (36)	36 [34]		- F20 fF (20)	+sNIT (24)	28 [24]		-NFA rF (14)	PSE (10)
Uncinia tenella	**[32]**			**[+dAG6 23]**	61 [36]		-F20 rF (33)	+sCYT (29)				
Tmesipteris obliqua	49 [42]	- MDN rF (26)	- FCX fR (13)	+sNIT (29)	47 **[49]**	- MDN rF (15)		+sNIT (23)	46 [45]	N	-F20 nC (13)	-sCYT (18)
Trochocarpa gunnii	29	-RFM nC (9)	-FCX rC (17)						54 **[55]**			-sPHW (29)
Rumohra adiantiformis	28 [19]	- RFM fF (18)		-cPPA (18)	35 [18]	- MDN rF (19)		+sALU (25)	64 [24]	- MDN fC (34)	- F20 fC (37)	
Pattern unclear												
Acacia melanoxylon	50 [22]	-MDN aF (25)	+F40 aF (16)		64	+MED nF (33)			52	-OGR nF (19)		
Anodopetalum biglandulosum	54 **[50]**	+ OGR aF (20)		**[-dFF3 22]**	38	- OGR rC (13)		-tAS4 (11)	46 [37]	- MRF rF (21)		+gGO3 (22)
Atherosperma moschatum	22 [19]	-MDN fC (9)		+sNIT (16)	43 [41]			-tTIN (16)	32 [23]	- RFM nC (13)	- F20 aC (12)	+sNIT (17)
Clematis aristata	**[15]**			**[+sCYM (10)]**	37 [15]	-RNF rC (33)		+sCAL (20)	**[16]**			**[+sNIT (12)]**
Ctenopteris heterophylla	**[33]**			**[+CRV(30)]**	22 **[27]**	- RNF fC (10)		+cPPW(15) **[+PPD 26]**				
Dianella tasmanica	48 **[56]**		-F40 rC (12)	-tSLP (17)	55 **[59]**		F60 rC (12)	-tSLP (16)				
Dicksonia antarctica	44 **[45]**		+F60 nC (13)	+sNIT (35)	42 [41]	-MDN aC (11)		+sNIT (25)	70 [47]		+ F60 nC (20)	+sNIT (20)
Eucalyptus regnans									19		+ F40 nC (10)	-tFLA (12)
Gahnia grandis	21	+MED aC (10)	+NFA aC (14)	-sPOT (9)	21	+MEA fC (9)	+NFA aC (13)	-sPOT (16)	54 [35]	-RNF nC (15)	+F20 aC (15)	+tCRV (16)

Table 4-J	all mature plots > 70 years old (n = 57)				Plots 70-109 years old (n = 34)				Old growth plots (n = 23)			
Species name	**pR²**	**MF**	**OV**	**Site**	**pR²**	**MF**	**OV**	**Site**	**pR²**	**MF**	**OV**	**Site**
Grammitis billardierei	44 **[50]**		-F20 rF (17)	-tPNC (29)	59 [57]			+sPOT (31)	54 [34]	-MDN aC (19)		+cRLW (21)
Hymenophyllum cupressiforme	33 [25]		-NFA rF (18)	-dAS4 (17)	34 [22]		+F40 fF (21)	-tAS4 (28)				
Hymenophyllum peltatum	23 **[26]**	+RNF aF (13)	+F40 nF (11)	+dAGE (14)	47 [41]		+F20 aC (15)	+dAGE (22)	54 [50]	-MED aF (21)		-tAS4 (31)
Hymenophyllum rarum	22 **[30]**		-F40 fC (12)	+sNIT(16) **-dAG4 36**	29 **[34]**			+sPOT (19)				
Histiopteris incisa	22	+MRF aF (18)	+F40 rF (15)	+sNIT (23)	26	+MRF aF (19)		+sNIT (26)	42 [33]	-OGR rC (12)	-F20 nC (9)	+cRLW (13)
Leptecophylla juniperina	24 [20]	+ OGR fC (8)	+F40 aC (12)	-cTMN (17)	23	+MED fC (7)	+F40 aC (14)	-cTMN (8)	20	+MDN nF (10)		+tTOP (7)
Melaleuca squarrosa	33	+MED fC (17)		+cTMN (24)	48 [30]	+RFM aC (12)		sPOT (21)				
Nematolepis squamea					22 [22]	+ MEA rF		- sNIT (15)	51 [45]		-F40 fC (12)	+tCRV (16)
Pimelea cinerea	46 [46]			-sGO3 (42)	43 [34]		-F20 fF (36)					
Tasmannia lanceolata	43		+F40 nF (28)		43	-MDN rC (30)	-F60 nC (27)		40 [29]	-RNF nC (19)		+cPPW (14)
Independent of LC metrics												
Cenarrhenes nitida	52 [49]			-cRWM (19)					49 [39]			-cTMX (23)
Eucalyptus obliqua	58 [52]			+tPNC (35)	55 **[56]**			-sNIT (27)	57 **[58]**			-tFLA (20)
Leptospermum lanigerum					**[25]**			**[-tNNS (29)]**				
Monotoca glauca	44 [42]			-dAGE (31)	43 [40]			+cTMX (19)	45 [43]			-tFLA (21)
Pteridium esculentum					**[19]**			**[+cTAM (20)]**				

4.11 Meta analysis of model results for plant persistence / dispersal groups

Table 4-K. Relative measures of Importance of mature forest metrics for species groups

Data derived from the Random Forests abundance models using all regrowth forest plots and the same candidate set.

		MFI species			Other species				Two group comparison	
		Ferns	**Long range dispersal**	**Short range dispersal**	**Ferns**	**Long range dispersal**	**Medium range dispersal (bradyspory)**	**Short range dispersal (soil seed bank)**	**All Silvicultural regrowth indicators**	**All Fire-sensitive Old growth indicators**
IVMA (Mod RFb)	Mean	11.6 ± 8.1	2.4 ± 5.4	**16.7 ± 19.4**	-2.0 ± 15.6	2.2± 16.0	7.5 ± 10.6	-6.6 ± 6.3	-1.6 ± 8.6	16.7 ± 19.4
	Median	13.5	0	**12**	-2	0.0	7.5	-9	0.0	12.0
H = 11.39 DF = 6 *P* = 0.08		a	ac	**a**	*	abc	*	b	H = 2.66 DF = 1 *P* = 0.10	

Chapter 5 Appendices

5.1 Correlations between site variables and LC metrics within silvicultural forests

Four site variables, important for explaining assemblage variation in silvicultural regrowth forests, were independent of all LC metrics (absolute Pearson's R all < 0.273, *P* all > 0.05). These variables were mean maximum temperature and all three soil variables pH, conductivity and soil nitrogen. In contrast silvicultural forest age was associated with LC:FF:1k, as well as all four PM metrics (0.273 < absolute Pearson's R > 0.341, *P* < 0.05). Precipitation in the driest week and fire frequency were weakly to strongly correlated with all LC and PM metrics. The strongest correlations observed for fire frequency were with both spatial scales of LC:BF (absolute Pearson's R >0.74, *P* = 0) and with both scales of LC:CY (absolute Pearson's R >0.54, *P* < 0.0001). The strongest correlations of mean precipitation in the driest week were with LC:FF:½k and LC:FF:1k (absolute Pearson's R >0.53, *P* <0.0001).

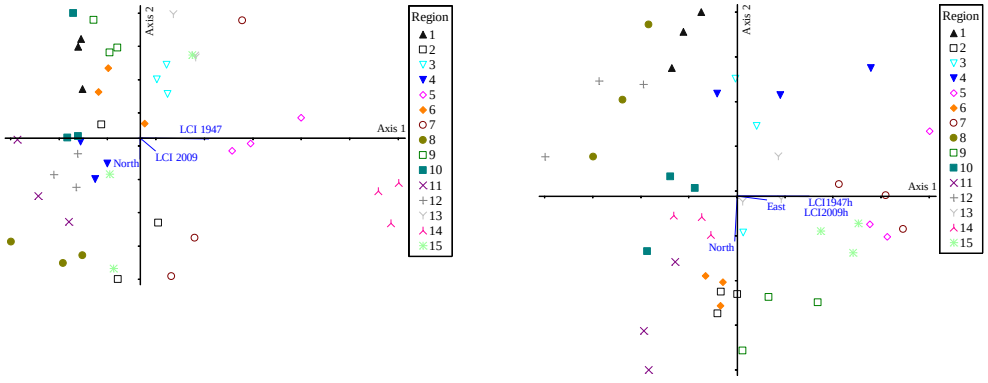
Almost all LCI and PM metrics were more strongly associated with each other than could be explained by chance variation (absolute Pearson's R >0.273, *P* <0.05).

5.2 Correlations between site variables and LC metrics within mature plots

None of the four soil variables most associated with mature forest assemblages (pH, conductivity, nitrogen and calcium) or the two temperature variables (mean annual temperature, and mean maximum temperature) were correlated with the LCI metrics (absolute Pearson's R < 0.0.23, *P* > 0.05). However, both rainfall variables (mean annual precipitation and mean precipitation in the driest week) were strongly correlated with the LCI metrics (absolute Pearson's R all > 0.0.38, *P* all <0.005).

Chapter 6 Appendices

6.1 Regrowth assemblage variation



a b

Figure 6-A. NMS ordination of regrowth subplot data (square root transformed cover data) overlaid with vectors for LCI scores correlated with species assemblage variation (100% scale, cut off R^2=17%). (a) Old field regrowth plots; (b) other regrowth plots.
The axes have been rotated to align with LCI 1947. For correlation of each axes with LCI see Table 6–A below.

Table 6-A. Results of the Correlations (Kendall tau) between NMS ordination axes and LCI scores

NMS Axis	Regrowth type	Axis correlation (R^2) with dissimilarity matrix	Axis correlation (tau) with LCI 1947	Axis correlation (tau) with LCI 2009
Axis 1	Old field	**0.469**	**0.267**	0.178
Axis 1	Other	0.298	0.240	0.312
Axis 2	Old field	0.280	0.078	-0.137
Axis 2	Other	**0.372**	**-0.387**	**-0.316**
Axis 3	Old field	0.111	**-0.292**	-0.109
Axis 3	Other	0.166	0.029	-0.119

6.2 Association between plant group richness and LCI

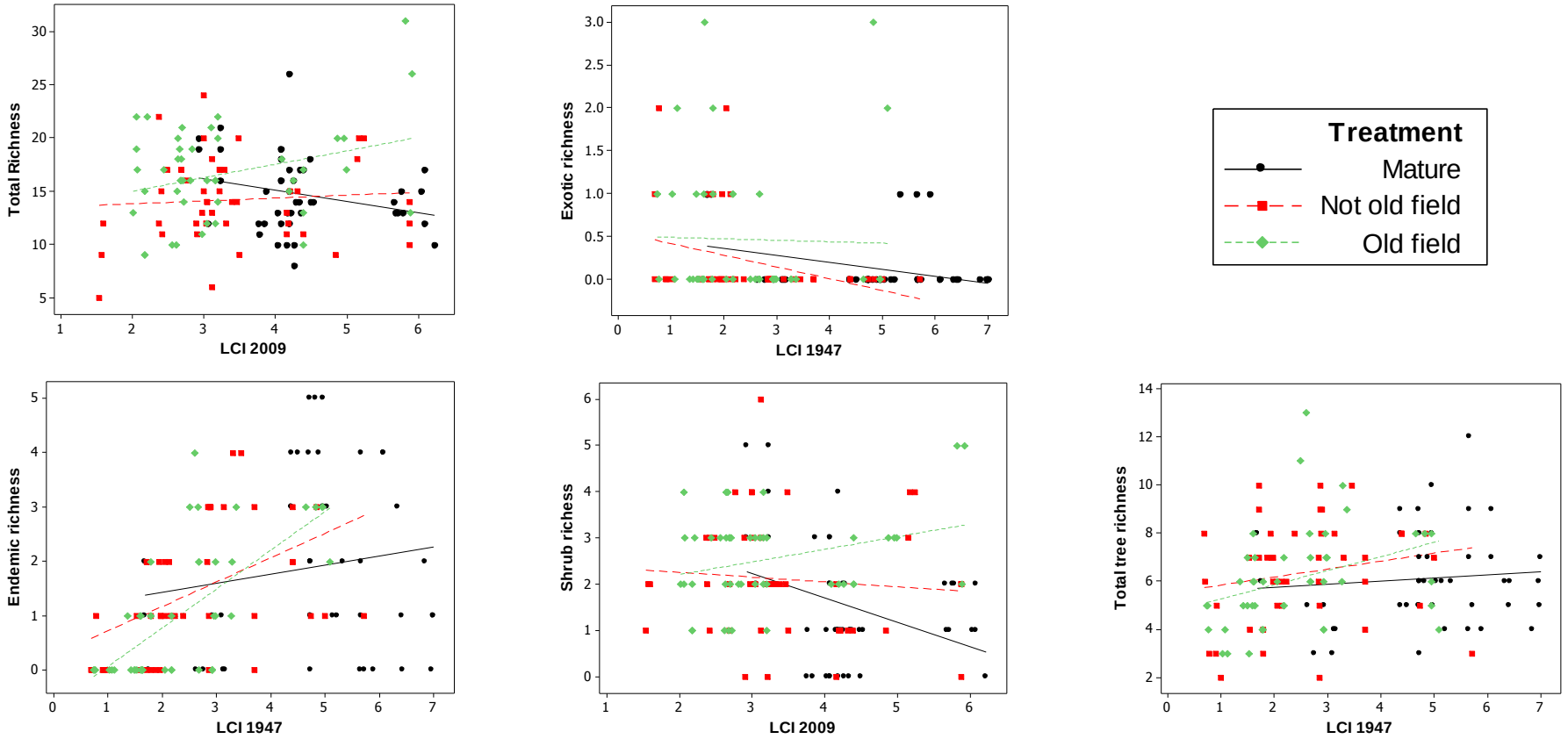


Figure 6-B. Scatter plots of richness levels of several plant species groups (including eucalypt species) (Y-Axis) against LCI scores (X-axis) for three forest types: mature forest, regrowth forest on old field sites and regrowth forest on other sites.

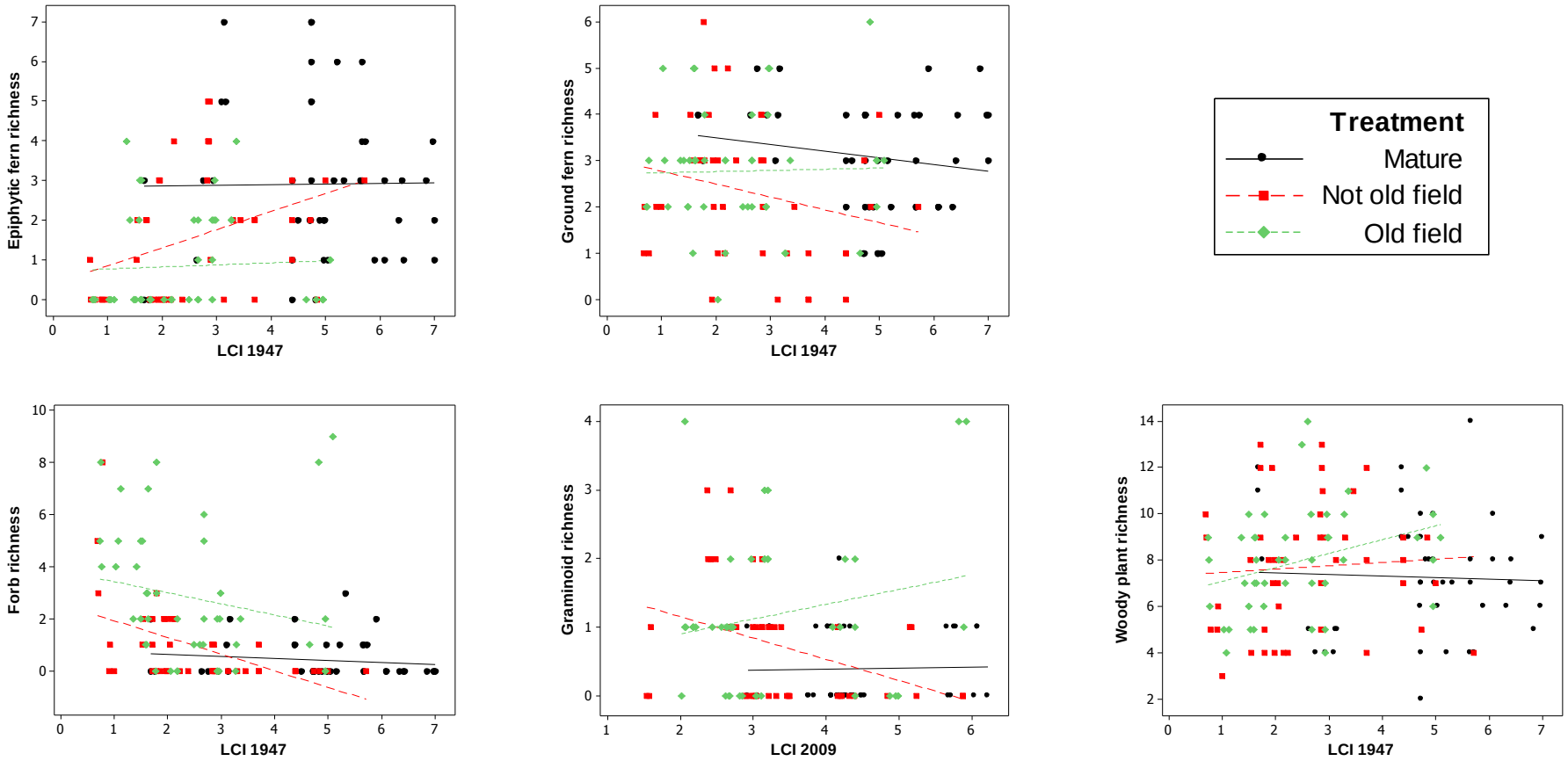


Figure 6-C. Scatter plots of richness levels of each life form class (excluding eucalypt species) (Y-Axis) against LCI scores (X-axis) for three forest types: mature forest, regrowth forest on old field sites and regrowth forest on other sites.

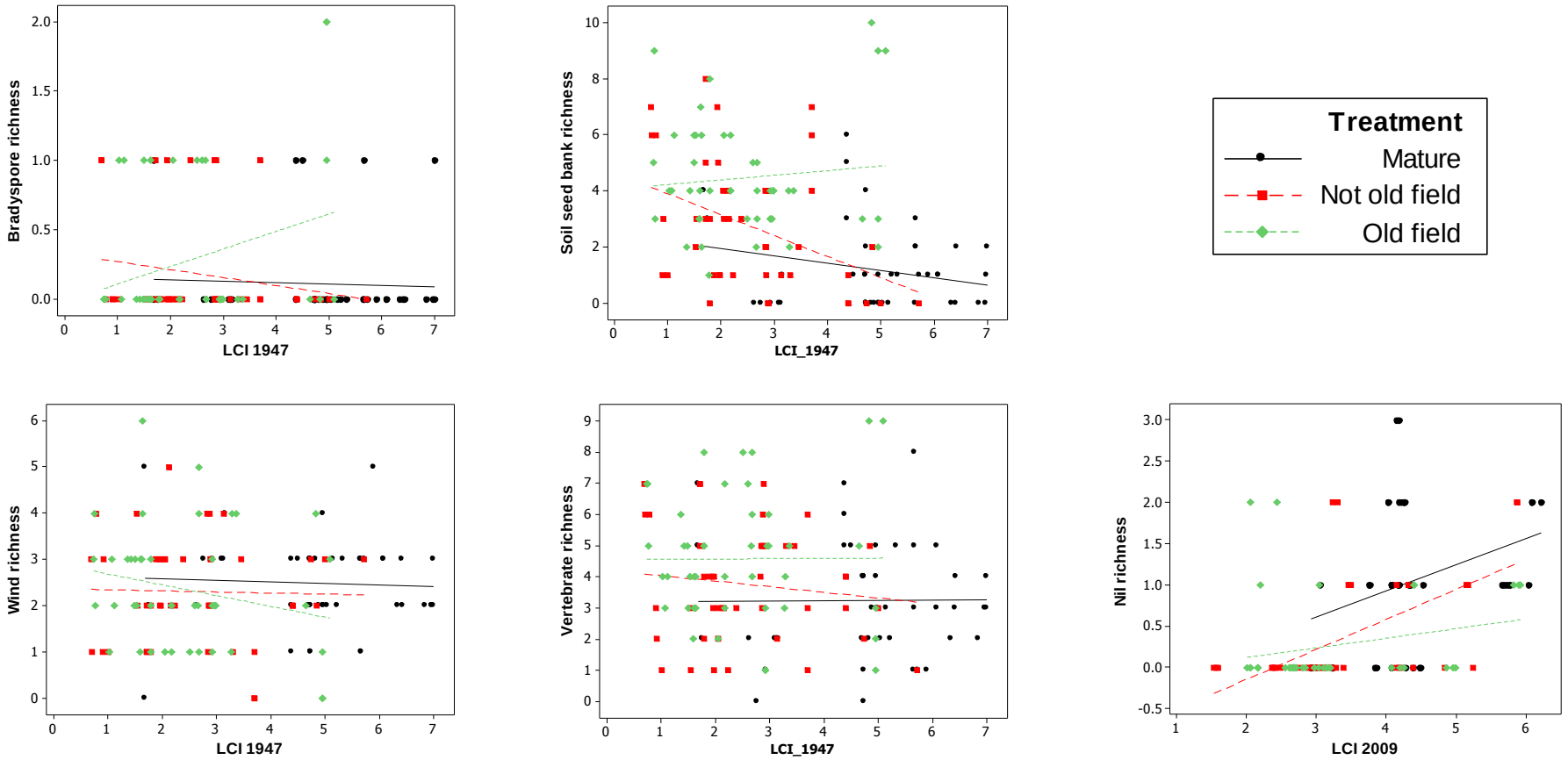


Figure 6-D. Scatter plots of richness levels of each spermatophyte dispersal / persistence class (excluding eucalypt species) (Y-Axis) against LCI scores (X-axis) for three forest types: mature forest, regrowth forest on old field sites and regrowth forest on other sites.

6.3 Association between plant group cover and LCI

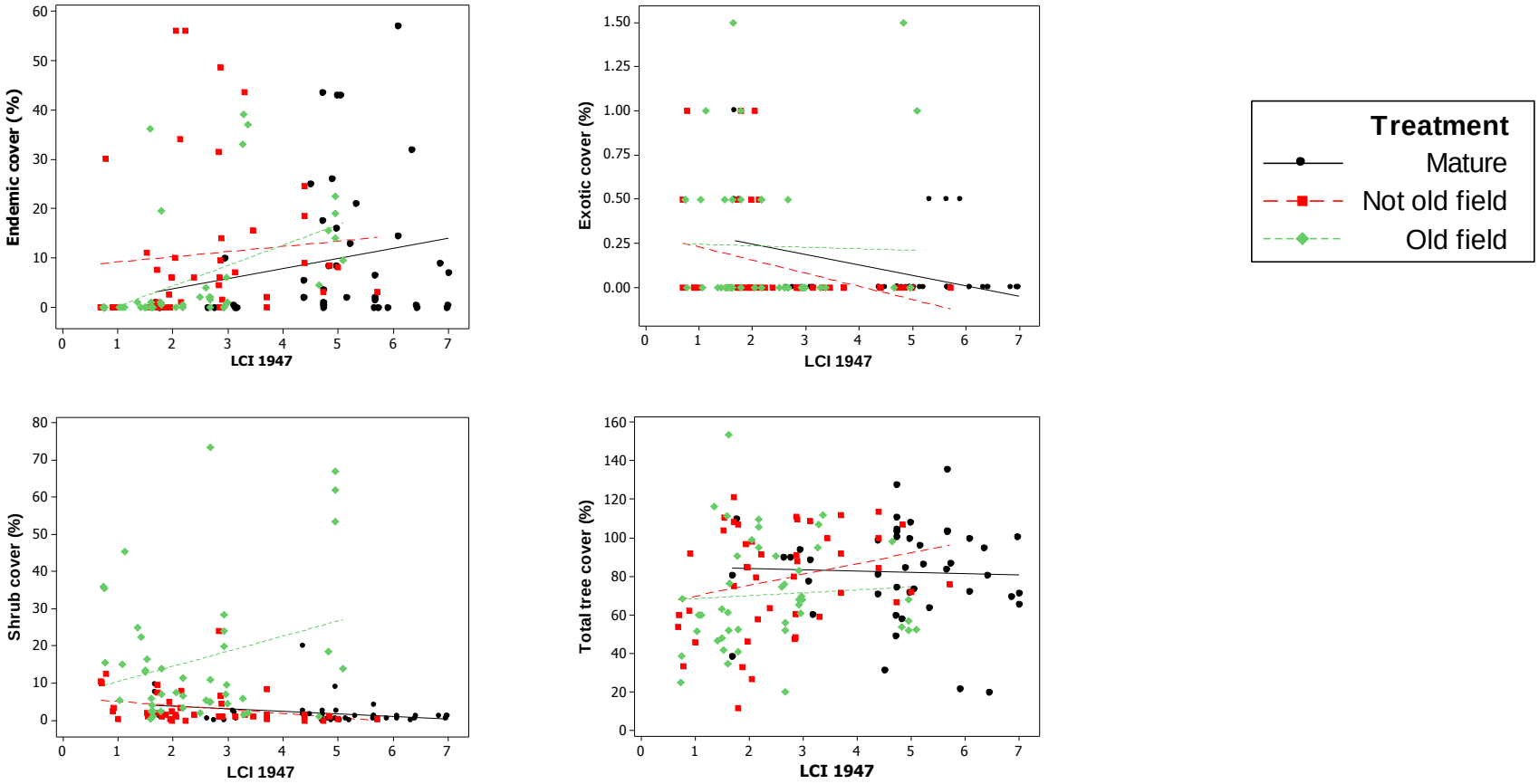


Figure 6-E. Scatter plots of cover levels for several plant species groups (including eucalypt species) (Y-Axis) against LCI scores (X-axis) for three forest types: mature forest, regrowth forest on old field sites and regrowth forest on other sites.

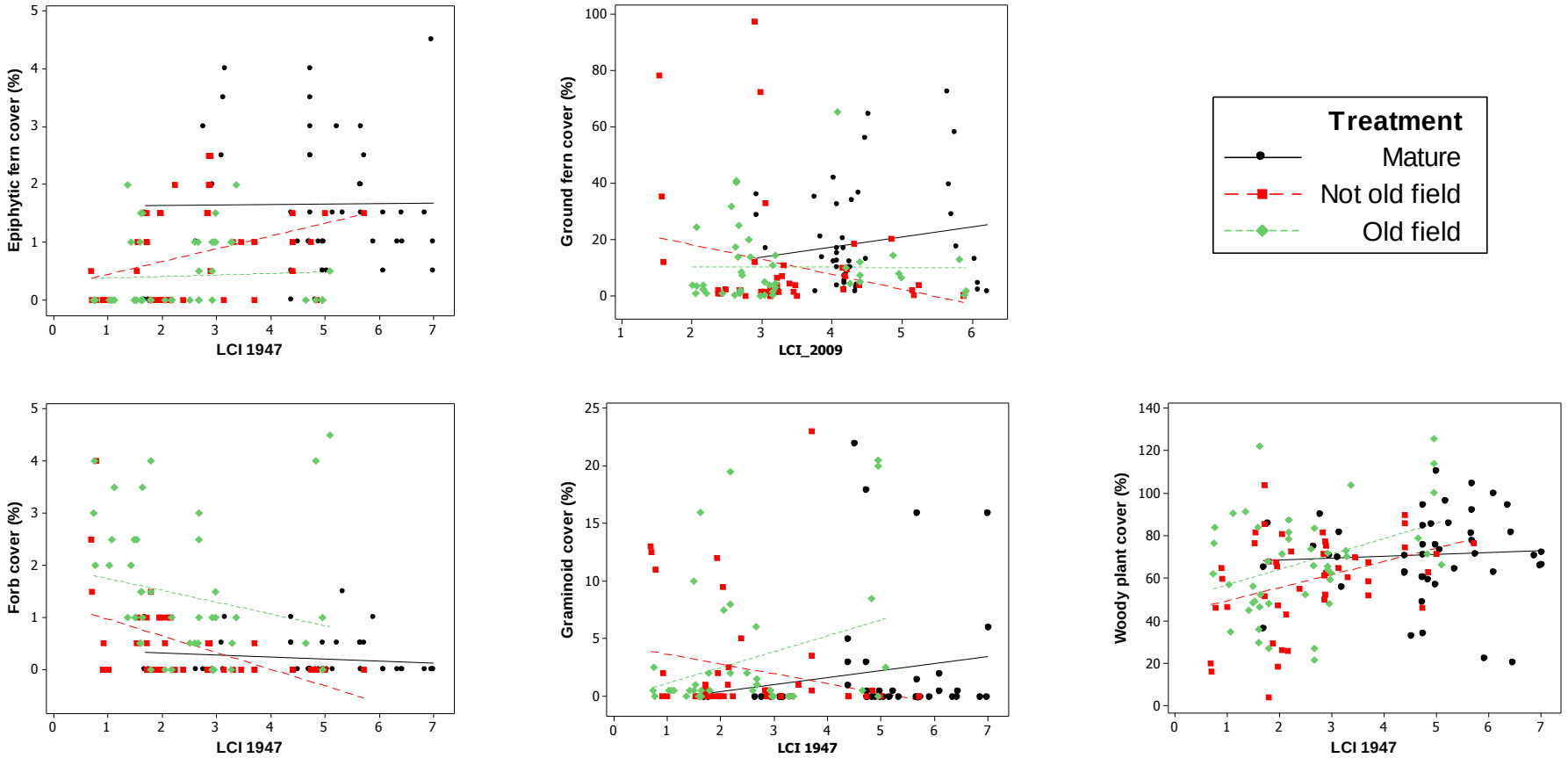


Figure 6-F. Scatter plots of cover levels of each life form class (excluding eucalypt species) (Y-Axis) against LCI scores (X-axis) for three forest types: mature forest, regrowth forest on old field sites and regrowth forest on other sites.

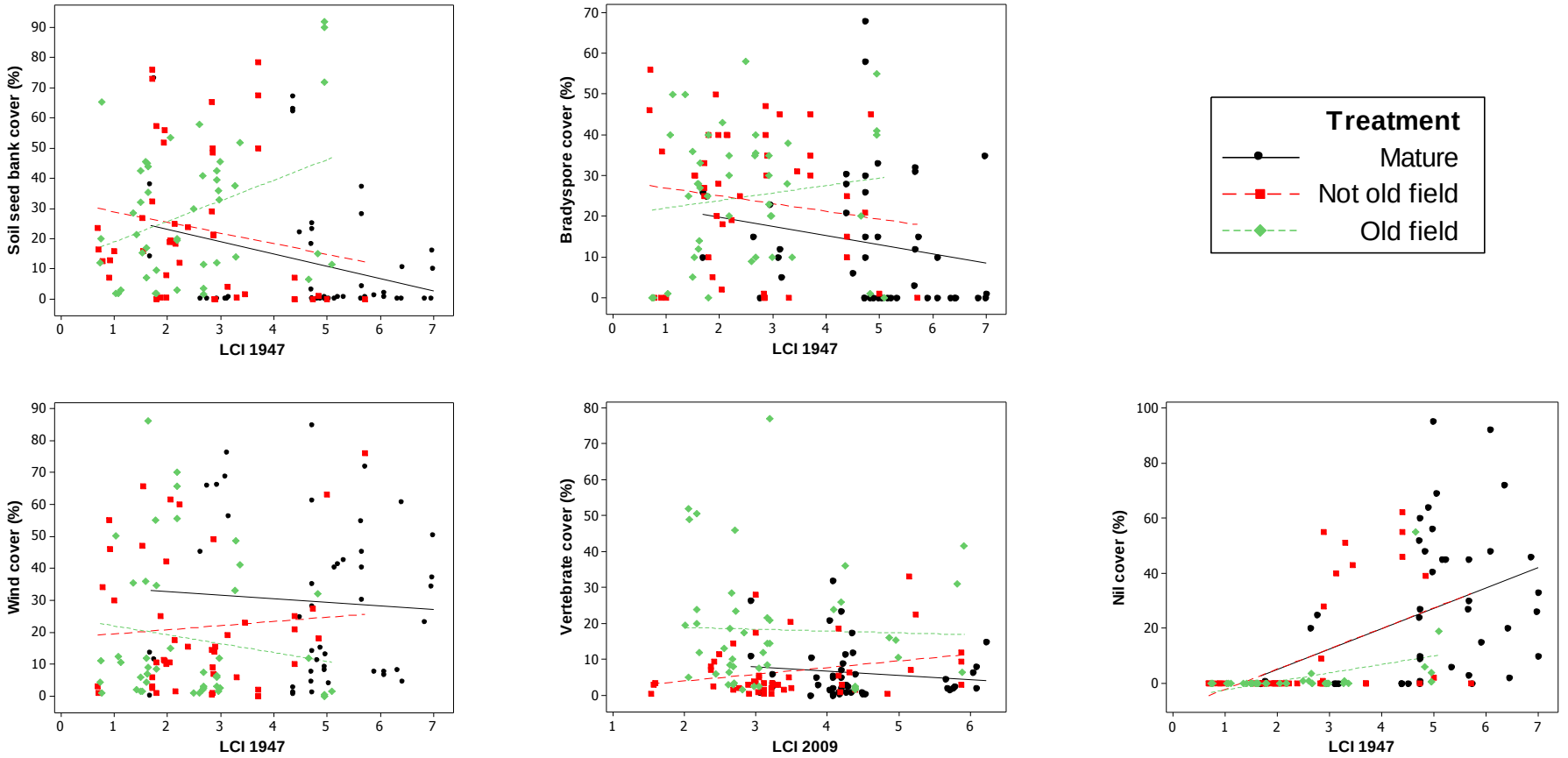


Figure 6-G. Scatter plots of cover levels of each spermatophyte dispersal / persistence class (excluding eucalypt species) (Y-Axis) against LCI scores (X-axis) for three forest types: mature forest, regrowth forest on old field sites and regrowth forest on other sites.

6.4 Regrowth forest assemblage similarity to mature forest

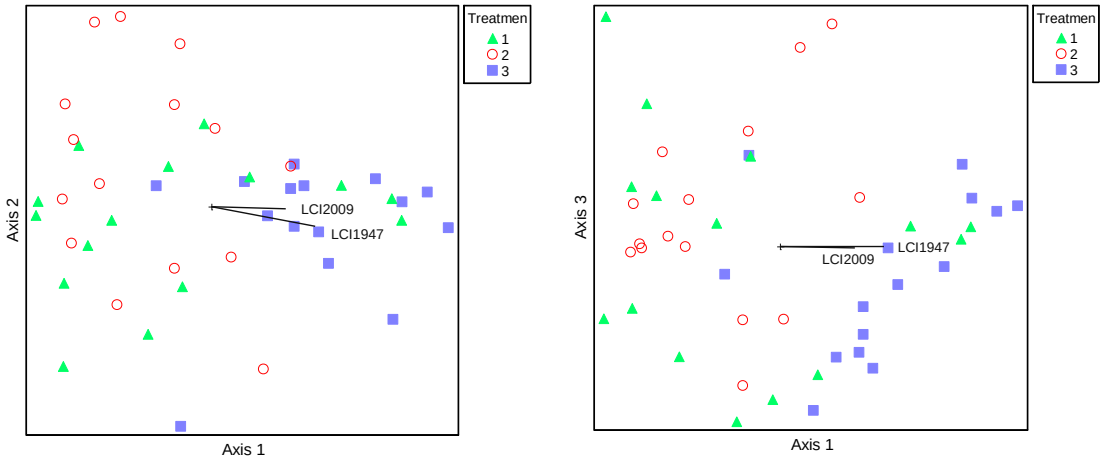


Figure 6-H. NMS ordination (square root transformed average cover data) of all plots showing assemblage variation by forest types (regrowth Treatments: 1 = other regrowth plots, 2 = old field plots; Treatment 3 = mature forest plots.

Notes for ordination: Vectors for LCI scores for 2009 and 1947 are superimposed on the ordination showing their association with assemblage variation (100% scale, cut off $R^2 = 35\%$). Ordination axes rotated to align mature forest plots with the first axis. Pearson's correlations between axes and original dissimilarity matrix: Axis 1, $R^2 = 35\%$; Axis 2, $R^2 = 22\%$; Axis 3, $R^2 = 24\%$. The stress of the final solution was 13.4%.

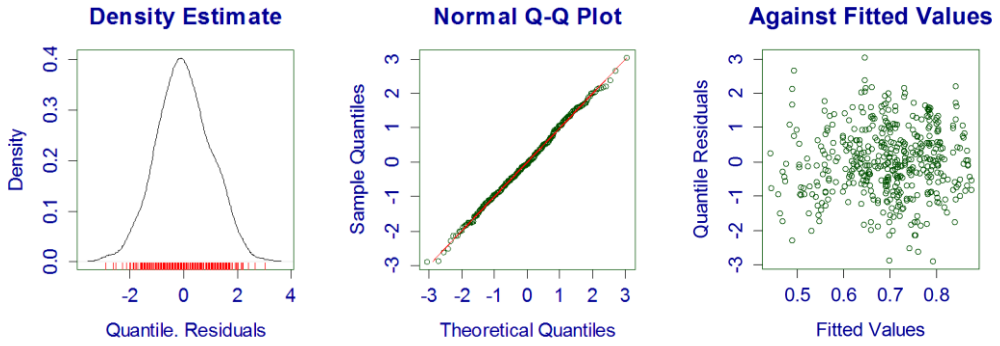


Figure 6-I. Residual diagnostic plots for linear mixed effect model for mean Bray-Curtis dissimilarity to mature forest (For model details, see Part A: Table 6–5).

Chapter 7 Appendices

7.1 Forest mapping

Combining current mapping and fire history data with vegetation height and intensity data captured by LiDAR and high resolution multispectral data such as RapidEye can be used to distinguish different forest understoreys. In preliminary studies, not previously reported in the present thesis, Random Forests modelling of the satellite imagery demonstrated capacity to distinguish between some forest understoreys, with the most difficult to distinguish being callidendrous rainforest understoreys from *Pomaderris apetala* closed-scrub. Visual inspection of LiDAR data provided evidence that the intensity of return signals would distinguish these two understoreys from each other. Data from the present project and other inventory survey data collected by Forestry Tasmania would be valuable for ground-truthing this potential discrimination.

7.2 Landscape context and disturbance differences in one year old silviculture and wildfire regrowth

7.2.1 Aim of study

Baker et al. (2013) studied the effects of adjacent vegetation and disturbance treatment on one year old regrowth at six aggregate timber harvest sites. Their analysis investigated general assemblage and species richness differences. They established that there were assemblage and total species richness differences depending on whether the regrowth had been subject only to fire or whether it had also been harvested prior to burning. They detected no differences in silvicultural regrowth depending on whether the adjacent forest had been burnt or not. Their data are re-examined here, to determine if plants grouped into early and late stage successional species classes respond in the same way to disturbance differences and landscape context.

7.2.2 Method

The six sites studied by Baker et al. included three within the study area of this thesis (Arve 23, Picton 07, and Esperance 81) and three within the Styx Valley (Styx 04, Styx 07 and Styx 18) a region less than 40 km to the northwest, in a similar geological and climatic zone. Their sampling design established replicate circular plots (100 m^2) in each of four treatments at each site:

F – unharvested and unburnt forest adjacent to harvest site (n =60);

SA – silvicultural regrowth adjacent to unburnt forest (n =60);

FB – forest burnt in regeneration burn adjacent to harvest site (n = 44);

SB: silvicultural regrowth adjacent to burnt but unharvested forest (n = 66);

Each of the forest plots (burnt and unburnt) was associated with a matching plot in the silvicultural regrowth, with additional plots established within some areas of silvicultural regrowth established adjacent to burnt forest. Using the results of indicator species analysis presented in Chapter 4, each species was allocated to one of five classes: silvicultural indicators, mature forest indicators, other pioneer species, other mature forest species or other unclassified. The other unclassified was allocated to orchids, eucalypts, and three species records for which the identification or status of the species was unknown. For each plot the richness was tallied for each of these classes and the sum of the two pioneer and mature forest classes also calculated. Class mid-points were allocated to each Braun-Blanquet cover index score and sum of the covers for each species class calculated for each plot.

To test responses, linear mixed effect modelling was undertaken by specifying the treatment as the only fixed effect factor with the six sites specified as a random effect factor. The linear mixed effect modelling was undertaken using Gamlss 4.3−0 (Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007; Stasinopoulos et al. 2014) within the R software platform (R Core Team 2014). For this data set the richness data were modelled using Poisson distribution family and the cover data (plus one) were log transformed and analysed specifying a normal distribution.

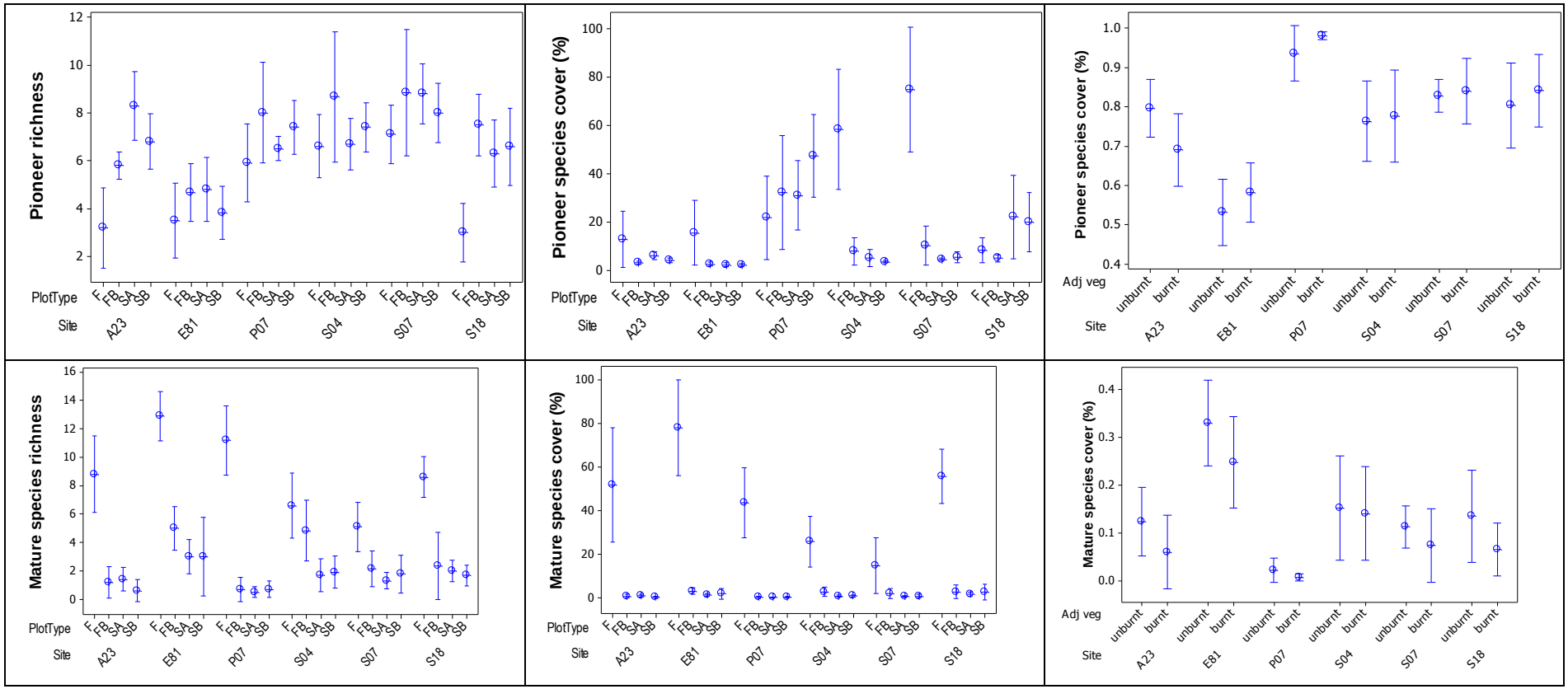


Figure 7-A. Mean and 95% confidence interval for species richness (far left) and cover (centre and far right) at six sites one year following regeneration portioned according to: pioneer species (above) and mature forest species (below) for four treatments F: unharvested unburnt forest adjacent to harvested plots; FB forest burnt in regeneration burn adjacent to harvest site; SA: silvicultural regrowth adjacent to unburnt forest; SB: silvicultural regrowth adjacent to burnt but unharvested forest (left and centre columns) and silvicultural regrowth adjacent to 'unburnt' forest and 'burnt' forest (right).

7.2.3 Are richness levels of pioneer and mature forest species in one year old silvicultural regrowth the same as regrowth burnt by wildfire?

As reported by Baker et al. 2013 there was no evidence that total richness levels varied within the silvicultural plots in association with whether the adjacent vegetation had been burnt or not (data not shown). Likewise the total pioneer species richness and cover levels also lacked any discernible association with adjacent vegetation treatment (Figure 7-A, Table 7-A), a result also obtained for the richness and cover of the two subgroups silvicultural indicators and other pioneers species. In contrast, there was evidence total richness and cover of mature forest species were lower in sites where the adjacent vegetation had been burnt (Table 7-A, Figure 7-A). Richness of mature forest indicator species was not associated with whether the adjacent vegetation had been burnt or not, although the *P*-value was small (t=-1.68, $P = 0.09$). However, the cover of mature forest indicator species was lower in silvicultural regrowth near a burnt forest edge (t = -2.29, $P = 0.024$).

Table 7-A. Results of linear mixed effect modelling to test for floristic responses to treatment (unburnt versus burnt vegetation adjacent to plot).

Floristic response	Coefficient for burnt adjacent)	Std error for burnt adjacent)	t-value	*P*-value
Pioneer species (all) Richness	-0.1199	0.1067	-1.12	0.263
Mature forest species (all) Richness	-0.4079	0.1632	-2.50	0.014
Pioneer species (all) Cover	-0.0171	0.1033	-0.17	0.869
Mature forest species (all) Cover	-0.2110	0.0698	-3.02	0.003

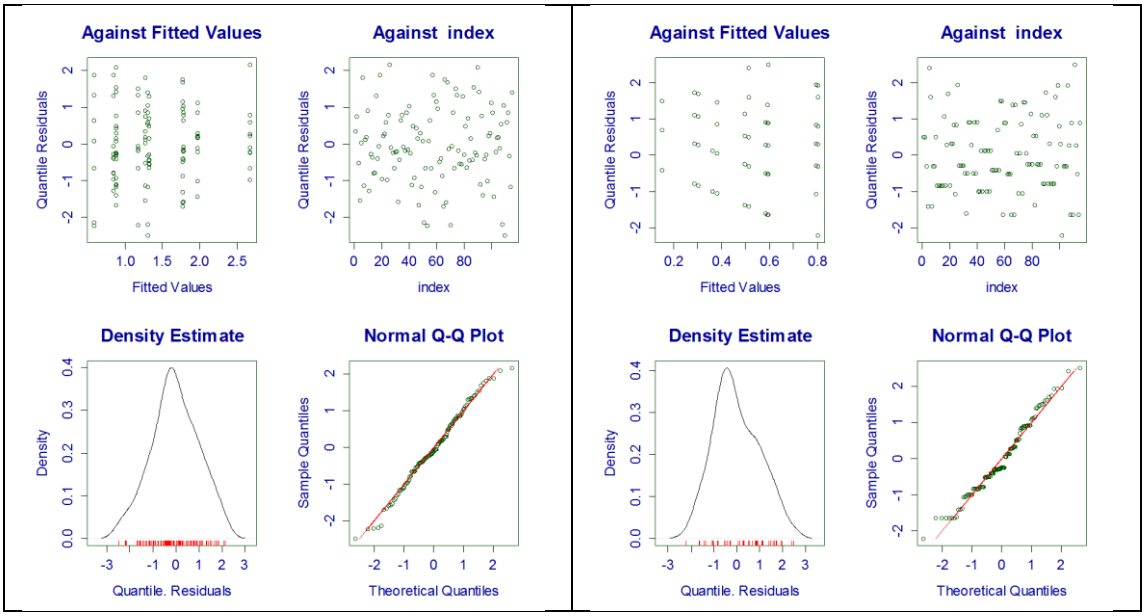


Figure 7-B. Residual diagnostic plots for model of mature forest species richness (left) and cover (right) in silvicultural regrowth predicted by treatment (adjacent forest burnt or not).

7.2.4 Do richness levels of pioneer and mature forest species in one year old silvicultural regrowth vary depending on their landscape context?

There was evidence that the richness and log transformed cover of mature forest species was lower in all silvicultural regrowth compared with the unharvested regrowth forest (Table 7-B). This result was obtained despite an anomalous observation at one site (Picton 07) of higher mature forest covers in the silvicultural plots adjacent to burnt forest than in either the silvicultural forest adjacent unburnt forest or the unharvested regrowth forest. The same results were obtained for the subgroup of mature forest indicator species (data not shown).

There was no evidence that cover or richness of pioneer species (silvicultural indicators or others) were more or less common in unharvested regrowth forest compared with silvicultural regrowth (Table 7-B).

Table 7-B. Results of linear mixed effect modelling to test whether floristic response in burnt but unharvested forest regrowth was different from harvested areas, including 1.areas adjacent to burnt forest and 2. areas adjacent to burnt forest.

Floristic response	Coefficient (± std error) 1. adjacent to unburnt forest)	t-value (*P*-value) 1. adjacent to unburnt forest)	Coefficient (± std error) 2. adjacent to burnt forest)	t-value (*P*-value) 2. adjacent to burnt forest)
Pioneer species (all) Richness	-0.1914 (± 0.3741)	-0.51 (0.61)	-0.4392 (±0.3673)	-1.20 (0.23)
Mature forest species (all) Richness	-1.0322 (± 0.3578)	-2.88 (0.005)	-1.0628 (±0.3514)	-3.02 (0.003)
Pioneer species (all) Cover	0.0776 (±0.1148)	0.68 (0.50)	0.0884 (±0.1127)	0.78 (0.43)
Mature forest species (all) Cover	-0.2678 (± 0.1023)	-2.62 (0.010)	-0.3402 (± 0.1005)	-3.39 (0.001)

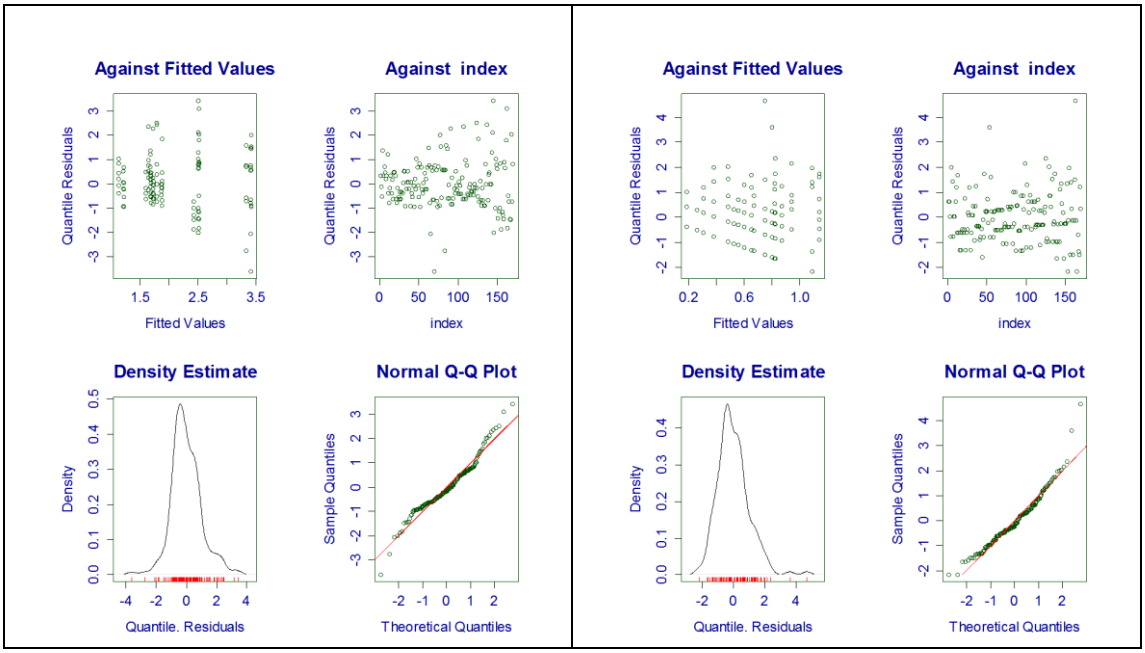


Figure 7-C. Residual diagnostic plots for model of mature forest species richness (left) and cover (right) in regrowth predicted by treatment (harvested adjacent to unburnt forest, harvested and adjacent to burnt forest or unharvested but burnt).

7.3 Successional dynamics in wet eucalypt forest

7.3.1 Pioneer species

7.3.1.1 First decade of forest re-establishment

Longitudinal studies spanning less than ten years immediately post-harvest have observed that forbs and graminoids are often the initial dominants. They establish a peak cover within six months to two years and mostly become less important or relatively inconspicuous within six years (Cremer and Mount 1965; Wapstra et al. 2003; Neyland and Jarman 2011). Many of the herbs in recently disturbed sites are rare or absent in mature forest communities (e.g. see Murphy and Ough 1997). The data set collected by Baker et al. (2013) also demonstrated this trend. Nine of the 15 taxa not present in adjacent unburnt forests were forbs, while another was a graminoid in the genus *Juncus*. Of the remaining taxa, all but two were short-lived shrubs or climbers. Only two trees, both relatively short-lived and from the genus *Acacia*, were not represented within the adjacent undisturbed forest community. However, even at just one year of age the regrowth in some parts of those six sites was already dominated by the trees, *Eucalyptus obliqua* and *Pomaderris apetala*, although the forb, *Senecio minimus* and the sedge, *Gahnia grandis* were the most frequently recorded species apart from *Eucalyptus obliqua* and had higher cover levels than most other species.

Taller plants such as disturbance loving ferns (e.g. *Histiopteris incisa* or *Pteridium esculentum*) and/or tall tussock sedges (e.g. *Gahnia grandis*) replace smaller herbs in importance within two years of logging (Cremer and Mount 1965; Wapstra et al. 2003; Neyland and Jarman 2011). Chronosequence data from Victorian *Eucalyptus regnans* forests also demonstrated that *P. esculentum* is one of the few species that distinguishes the composition of three to six year old silvicultural regeneration from older age classes.

The light-demanding, fast-growing woody pioneer plants establish rapidly after logging (Cremer and Mount 1965; Murphy and Ough 1997; Wapstra et al. 2003; Neyland and Jarman 2011). These may include wind-dispersed Asteraceae tree

species (*Cassinia* spp. and *Ozothamnus* spp.), and species with long-lived soil stored seed banks (e.g. *Acacia* spp., *Nematolepis squamea, Pomaderris apetala,* and *Zieria arborescens*). Within a few years the woody pioneer species exceed the height of other life forms and establish dense cover (Cremer and Mount 1965; Wapstra et al. 2003; Neyland and Jarman 2011).

A chronosequence data set from Victorian *Eucalyptus regnans* forest shows rapid establishment of shrubs and trees in the first decade and a half (Serong 2007). The species that distinguish the floristic composition of youngest regrowth age classes in Victoria from forests more than 20 years since disturbance include the pioneer shrubs *Cassinia aculeata*, *Correa lawrenceana*, *Olearia phlogopappa,* and the trees *Acacia dealbata* and *Prostanthera lasianthos* (Serong and Lill 2008). These five indicator species peak in the 11-15 year age class.

Only seven sites under 10 years in age (4-8 years) were examined in the present thesis, five of which were part of the balanced design used to study mature forest influence along the 200 m gradient (Chapter 3). The youngest sites were already past the point of herb dominance, but pioneer forbs, graminoids and other short-lived light demanding species were still present. The pioneer trees and shrubs formed the tallest strata over a varied ground cover of pioneer shrubs, ferns and/or the sedge, *Gahnia grandis*. Of the 26 flowering herbs (forbs, grasses and other graminoids) in the mature forest influence data set, 20 were most abundant within the young sites. Sixteen were not recorded at all in older silvicultural regrowth or in any of the adjacent mature forests.

Several studies have found the community re-establishment in wet eucalypt forest is associated with differences in response to both the pre-disturbance community and the intensity or resonance time of disturbance (Jordan et al. 1992; Lindenmayer and McCarthy 2002; Turner and Kirkpatrick 2009; Neyland and Jarman 2011). Neyland and Jarman (2011) observe that the regeneration after harvesting of wet eucalypt forests which substantially lacked rainforest species in their understoreys before harvesting had almost completely recovered their pre-disturbance floristic composition within ten years of regeneration. However, after nearly ten years following regeneration, the silvicultural regrowth composition in areas that had been

previously occupied by mixed forests still did not show any close resemblance to pre-logging communities (Neyland and Jarman 2011).

Average total species richness is lower for harvested and burned regrowth than for that burned but not logged (Baker et al. 2013). Pioneer bradyspore species such as *Leptospermum* and *Banksia* recovered better in the burnt but unharvested sites, because the standing dead trees of these species released seed following the fire, whereas in harvested areas they had been killed and released seed that was then killed by the fire. Baker et al. (2013) also observe that there are other pioneers, such as the fern *Pteridium esculentum* and the forb *Senecio minimus,* which have greater cover in harvested areas compared with unharvested burnt areas. Consistent with other studies they also conclude that harvested regrowth is more homogenous than the regrowth within unharvested areas (Baker et al. 2013). However, when their data were re-examined no evidence was found to suggest that richness or cover of the pioneers varied been sites that had been harvested and then burnt and those that had only been burnt (Appendix 7.10.1).

The colonisation by eucalypts is strongly associated with burn intensities, with the highest densities and fastest growth rates occurring where intense heat has killed much of the seed in the soil seed bank and provided an ash-bed rich in minerals (Gilbert and Cunningham 1972; Cremer et al. 1978; Hindrum et al. 2012). Hindrum et al. (2012) reported that ash-bed areas in two year old silvicultural regrowth are characterised by the lowest species richness levels, as well as being characterised by the presence of the forb *Senecio minimus.* Noticeably absent from ash-bed areas are coppicing plants, species characteristic of low fertility acid-soils and species that germinate from the soil seed bank, including *Gahnia grandis, Nematolepis squamea, Monotoca glauca, Bauera rubioides* and *Pteridium esculentum* (Hindrum et al. 2012).

Hindrum et al. (2012) also note that total species richness levels were low in areas where soil had been compacted by machinery and where the tussock sedge, *Gahnia grandis,* had its greatest cover. In contrast, the highest species richness levels were reported for areas where litter was incompletely burnt and areas that not been burnt. They found species germinating from the soil stored seed bank were most common in soils where mineral earth has been exposed by the fire (Hindrum et al. 2012).

Data from one year old regrowth had a mean plot richness from four to nine pioneer species was recorded across six sites (re-examination of data from Baker et al. 2013, Appendix 7.10.1). The adjacent forests, which were not selected on the basis of their understorey, ranged from three to seven species per plot (Appendix 7.10.1). The mean pioneer richness levels observed in the four to eight year old silvicultural regeneration sites in the present study were not much higher than the one year old silvicultural regrowth of Baker et al. (2013), with a mean of nine species being recorded at four of the sites, and a mean of twelve pioneer species in the other. The mature forests adjacent to the regrowth sites in the present study had much lower levels of pioneer richness, varying from a mean of only two to four species per plot.

7.3.1.2 Older regrowth forest (20-50 years)

Based on anecdotal information and data from ring counts (e.g. Mount 1964), longitudinal and chronosequence data, survival rates within wet eucalypt forest communities maybe less than 50 years for many of the small understorey trees and shrubs (e.g. *Zieria arborescens*). Hence, by 40-50 years following disturbance it would be expected that richness and diversity of pioneers would already be reduced compared with younger communities.

The sites examined in the present thesis provided evidence that pioneer species richness and relative abundance did decline between four and 45 years since regeneration. Silvicultural indicator species as a group contributed most to the age-related decline in pioneer species richness. In contrast, models of abundance for individual species within silvicultural forests provided evidence that, among the common pioneer plants, almost none demonstrated either a positive or negative association with age within the 4–47 year old regeneration. The exceptions to this generalisation were the abundance models for *Gahnia grandis*, *Zieria arborescens*, *Senecio minimus* and *Dianella tasmanica;* these demonstrated a reduction in cover with age. Between the different dispersal and persistence groups of pioneer species, the age trend was not consistent. The species groups that did not demonstrate strong decline with age in silvicultural regrowth were also those that were more important within the old field communities (soil-stored seed plants, vertebrate dispersed seed plants, and to a lesser extent bradysporous plants). Although these groups include

many species that are relatively short lived in shady conditions (e.g. *Gahnia grandis*, *Zieria arborescens*), they often persist even in mature forests at much lower densities. Hence using richness (number of plants per unit area) as a means of determining if pioneers species or sub-groups are becoming less common in the community through time may miss important changes in abundance within some species of this group.

The lack of observed changes in richness of some groups of pioneer species in the first 45 years does not prove the absence of species turn over, within these groups. It is probable that there was some replacement of species, such as short-lived herbs, by recruitment of other species. This could occur as plants grow larger, or spread vegetatively, increasing the probability of being captured within the 10 x 10 m samples. It might also result if recruitment by seed germination continues beyond the first decade. The greatest evidence that species replacement and expansion may be occurring is provided by the polynomial relationship with age for richness of wind dispersed species, which demonstrated an increase in richness between the first and third decade of regeneration, after which it declined. This trend, and the observation of some short-lived pioneer species in mature forest (Figure 7-D) confirms the observation of Ashton (2000) that recruitment of pioneers does occur, at least occasionally, beyond the first decade following intense disturbance. However, recruitment of new species into the patch is likely to be low, and associated with light gaps generated by tree deaths, tree falls and other events that lead to soil disturbance.

The inclusion of data for sites that for environmental reasons were likely to be unsuited to the establishment of the species in the individual species abundance models resulted in zero inflated data sets. This may have obscured more subtle trends in the demographic patterns of species abundance. Surveys using more precise methods of cover estimation in longitudinal study sites are needed to determine pioneer species dynamics with greater certainty.

Hickey (1994) and Turner and Kirkpatrick (2009) provide separately studies of 30 to 40 year old wet eucalypt forest comparing the abundance of species in sites regenerated from wildfire with those in harvested sites. Among the pioneers that were more abundant or frequent within the silvicultural regrowth were *Acacia dealbata* (soil stored seed), *Blechnum nudum* (ground fern), *Coprosma quadrifida* (vertebrate

dispersed), *Gahnia grandis* (soil stored seed bank), *Leptospermum scoparium* (a bradyspore), *Pomaderris apetala* (soil seed bank) *and Tasmannia lanceolata* (vertebrate dispersed). Total species richness levels were higher in wildfire regenerated regrowth forest than logged and burned regrowth forest (Turner and Kirkpatrick 2009), and there was also evidence of greater frequency or abundance of *Monotoca glauca* (soil stored seed bank), *Nematolepis squamea*, *Pimelea cinerea* (vertebrate dispersed seed) and *Prostanthera lasianthos* (soil stored seed bank).

7.3.1.3 Older forests (> 50 years)

The life spans of pioneer species vary greatly. *Eucalyptus regnans* may live for up to about 500 years (Wood et al. 2010) and several of the important sub-canopy trees may also live for about a century (e.g. *Pomaderris apetala*). However, most have shorter life spans and it is expected that the pioneer species will be rare in old growth communities.

No longitudinal study sites have yet reported the sequence of compositional change from pre-disturbance all the way through to older silvicultural ages (~30 years). However, Ashton (2000) documented changes observed for one area in Victoria over a 48 year period, commencing monitoring in forest understoreys between 25 and 50 years since last fire, and ending when they were nearly 75 and 100 years respectively. The trend across all sites was a reducing density for the majority of tree species, with several becoming absent in the visible vegetation by the end of the period, although the seeds of those that disappeared remained present in the soil (Ashton 2000).

Ashton (2000) found that only a small number of the least light demanding and long-lived species were observed to increase in abundance over time of which most were classified for the purpose of this study as mature forest species. However, the shrub/small tree, *Coprosma quadrifida*, classified here as a pioneer, increased its cover by root suckering. Ashton and Turner (1979) reported that the light compensation point for *C. quadrifida* was 183 lux, intermediate between the keystone rainforest tree species (*Atherosperma moschatum* and *Nothofagus cunninghamii*) and the keystone mesophyllous pioneer trees (*Bedfordia salicina* and *Pomaderris aspera*). *P. aspera* (occupying the same functional role as the closely related *P. apetala*)

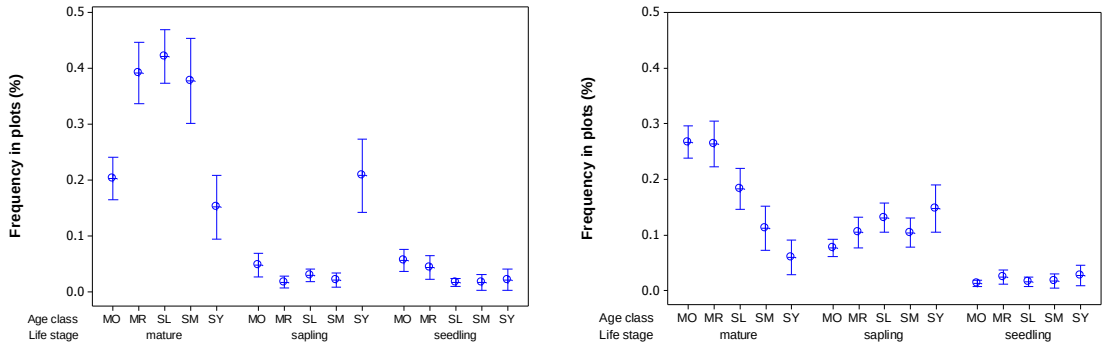


Figure 7-D. Mean frequency (with 95% confidence interval) of occurrence of ten common pioneer tree species (left) and mature forest tree species (right) within patches* by life stage and forest age class

* Frequency of occurrence calculated as the number of subplots (10 x 10 m) in which the life-stage of each species was recorded divided by the total number of subplots measured for the site. Sites were mostly sampled within 50 x 50 m areas but all data from the mature forest influence study were included, comprising samples along 200 m transects.

Age classes: **MO** (n = 36): Forest with old growth trees, disturbed by wildfire pre-1898;
MR (n = 24): Forest with regrowth eucalypts and old growth trees, Disturbed by wildfires pre-1960:
SL (n = 34): Late stage silvicultural regrowth regenerated between 1960 and 1979,
SM (n = 10): Mid stage silvicultural regrowth regenerated between 1980 and 1999;
SY (n = 7): Young silvicultural regrowth regenerated since 2000.

Life stages: **Mature**: Full sized tree or evidence of sexual maturity
Sapling: Resprouting plant, or small plant greater than ~15 cm in height which is not considered to be sexually mature;
Seedling: Plants or coppice, less than ~15 cm tall

Pioneer species: *Acacia dealbata, Acacia melanoxylon, Acacia verticillata, Bedfordia salicina, Cassinia aculeata, Coprosma quadrifida, Cyathodes glauca, Leptospermum scoparium, Monotoca glauca* and *Nematolepis squamea*.

Mature forest species: *Anodopetalum biglandulosum, Anopterus glandulosus, Aristotelia peduncularis, Atherosperma moschatum, Cenarrhenes nitida, Eucryphia lucida, Nothofagus cunninghamii, Olearia argophylla, Phyllocladus aspleniifolius* and *Pittosporum bicolor.*

was observed to successfully colonise a patch of senescent trees in an area it had not previously occupied, despite being a light-demanding species (Ashton 2000). Nevertheless, Ashton (2000) predicted that *P. aspera* would ultimately be eliminated from the visible vegetation if the forest remained undisturbed by fire.

In the present study area, seedlings of *Pomaderris apetala* were observed in late-stage silvicultural regrowth or older forests only twice. One instance was in a canopy gap being created by the senescence of 44 year old *P. apetala* trees, die-back presumed to be in response to infection by a fungal pathogen. Species commonly represented in mature forests as seedlings or young plants, in the absence of mature plants, included *Acacia melanoxylon, Clematis aristata, Coprosma quadrifida, Monotoca glauca*, *Pimelea drupacea* and *Zieria arborescens*. All of these species, although more abundant and frequent within young regrowth forest have the capacity to occur in rainforest (Jarman et al. 1984). An analysis of the prevalence of seedlings and saplings for ten of the most commonly occurring pioneer trees demonstrates that pioneer seedlings were more prevalent in the older age classes than silvicultural age classes. However, this trend was driven mainly by the inclusion of *Coprosma quadrifida* and *Acacia melanoxylon* among the top ten most common pioneer trees. The prevalence of mature plants of common pioneer species was lower in the old growth forests compared with all other age-classes except the youngest silvicultural regrowth (Figure 7-D). Seven of the ten common pioneer species contributed substantially to the presence at lower frequencies of pioneers within the old growth forests. The three common species rarely found in these forest age classes were *Bedfordia salicina, Cassinia aculeata* and *Leptospermum scoparium.*

Despite life spans that should exclude them from old growth forest communities, many pioneer species remain present in these mature forest communities, and while benefiting from disturbance are able to occupy rainforests, albeit at lower abundance and richness levels compared with younger forest age classes. The observation that the pioneer species reduced in cover and richness in these forests is in keeping with other data sets for this region such as that of Doran et al. (2003). A re-examination of the data set for the Victorian *Eucalyptus regnans* forest chronosequence (Serong 2007) failed to demonstrate such clear reductions in richness and abundance of pioneer species as a general group (data not shown). Nevertheless, the group of five

species that were indicators of the youngest regrowth classes had their lowest richness and abundance levels recorded in the old growth forest. The 61 year old regeneration also had significantly lower mean richness levels for these species (11–15 year mean richness = 4.7 ± 0.5; mean richness in 61 year regrowth 3.8 ± 1.1: one-way ANOVA: df =1, MS = 5.04, F = 7.44, *P* = 0.012).

The keystone pioneer species of Victorian *Eucalyptus regnans* forests, *Pomaderris aspera* was present in greatest abundance in 60 year regrowth but was also still common in old growth plots (Serong and Lill 2008). Likewise, the cover of *P. apetala* peaked within the forests sampled for the present thesis being most abundant between 70 and 100 years of age, although only in areas with higher pH. It was much rarer within the old growth forests, its occasional presence demonstrating its capability of regenerating in localised disturbance gaps, despite relatively low light levels.

7.3.2 Mature forest species

7.3.2.1 First decade

Cremer and Mount (1965), Wapstra et al. (2003) and Neyland and Jarman (2011) all reported that rainforest and other later stage species including *Olearia argophylla* were much less frequent and abundant compared with herbaceous and woody pioneer species in the first ten years following timber harvesting. Neyland and Jarman (2011) also observed that the abundance of rainforest species varied greatly within and between sites. They noted rainforest species were most abundant at sites where they had been common in pre-disturbance communities, particularly where they had been able to recover by resprouting (Neyland and Jarman 2011). Jordan et al. (1992) observed that rainforest species regenerated more quickly in the first decade following harvesting in areas that had not been burned or had been less intensely burned compared with recovery rates after high intensity fire.

The mean richness for mature-forest affiliated species in one year old silvicultural regrowth varied between a half and three species near adjacent unburnt forest areas (Appendix 7.10.1). By four to eight years since regeneration, means ranged between four to seven mature forest species.

In the data set of Serong (2007), ten plant species were missing from their youngest two age classes (3–15 years), but only three of these were represented in more than two of the mature forest plots (> 61 years old). Species absent from the youngest silvicultural regrowth included the rainforest trees *Atherosperma moschatum, Nothofagus cunninghamii* and the climber *Parsonsia brownii*. Serong and Lill (2008) observed the lowest mean total species richness levels in the youngest silvicultural regrowth, although their comparisons were potentially compromised by the merger of all grasses into one taxon and all other graminoids into another.

7.3.2.2 Older regrowth forest (20-50 years)

Within the third decade since regeneration, mature forest species richness levels were still low at two sites (means of two and three mature forest species near the boundary of mature forest) but three sites had mean richness levels for these species of between eight and fifteen. There was no evidence that near the mature forest edge, richness levels had increased by the fifth decade with mean richness levels only varying between seven and eleven species. The modelling results provided evidence that MFI richness increased most rapidly in the first 30 years and accumulated more slowly after that time, although the extraordinary recovery of rainforest species by coppicing at one of the sites may have skewed these results somewhat.

The silvicultural regrowth forest was also demonstrably more similar to adjacent mature forests in the fifth decade following regeneration compared with the first decade. A chronosequence of logged sites in the wet forests of East Gippsland (Williams 1995; Attiwill et al. 2014) also demonstrated that silvicultural regrowth becomes floristically more similar to mature forest as it ages. The rate of succession within forest types and taxon has been shown to vary greatly. Baker et al. (2015, in press) observed only small floristic differences between late-stage silvicultural regrowth and adjacent Douglas-fir forest in Washington state. Likewise, although the plant communities of the 45 year old regeneration in the Southern forests still showed considerable differences from mature forest, in these same sites the ground active beetles had assemblages that were difficult to distinguish from those of the adjacent mature forest (Fountain-Jones et al. 2015).

Within the abundance models of individual species (chapter 4), age was an important predictor for several mature forest species particularly the epiphytic ferns, *Dicksonia antarctica* and other rainforest plants such as the shrub *Aristotelia peduncularis* and the tree *Olearia argophylla*. Among the mature forest species that were less frequently recorded in regrowth forests by Hickey (1994) were *Anodopetalum biglandulosum, Atherosperma moschatum, Eucryphia lucida, Nothofagus cunninghamii, Pittosporum bicolor,* many of the epiphytic fern species, and *Blechnum wattsii*. All these species were also identified as indicators of mature forest on the basis of data collected for the present thesis.

Hickey (1994) also found that the epiphytic ferns were all observed more frequently in sites regenerated by wildfire compared with harvested areas, although not all statistical test results provided evidence for a difference in mean frequencies. Rainforest trees that were more frequent in mature forest compared with regrowth forest were also usually more common in wildfire regrowth compared with silvicultural regrowth but none achieved *P*-values of less than 0.05 in the study by Hickey (1994). The results of Turner and Kirkpatrick (2009) did not differ substantially from those of Hickey (1994) but they did detect a higher mean abundance of *Eucryphia lucida* in the wildfire regrowth. Contrary to the trends observed by Hickey, Turner and Kirkpatrick (2009) reported a higher mean abundance of both *Nothofagus cunninghamii* and *Olearia argophylla* within the logged sites. The conclusions that both authors drew from their respective data sets was that although there were differences in responses by vascular plants to timber harvesting compared with wildfires, the majority of species were more influenced by differences in moisture, temperature and soil fertility (Turner and Kirkpatrick 2009). These authors were basing their assessment on presence-absence data, which may be less sensitive to more subtle population changes than abundance data. However, compositional differences determined using cover abundance data from Victorian wet forest a decade after regeneration were similar to those reported in the Tasmanian studies, although the Victorians were able to detect reduced populations of both ground ferns and tree ferns following timber harvesting (Ough 2001). Although they noticed the abundance of resprouting rainforest trees, including *Olearia argophylla* and *Bedfordia arborescens*, was less following timber harvesting due to the added

mechanical disturbance, the differences were not great enough to register a statistically significant difference (Ough 2001). Nevertheless changes in the demographic structure of populations of long lived species such tree ferns and the rainforest tree *Olearia argophylla*, which would normally resprout rapidly after fire, also has implications for the recovery of epiphytic ferns (Mueck et al. 1996; Ough and Murphy 1996; Ough 2001). None of these studies investigate the impact of disturbance frequency/harvesting rotation on the recovery of these communities.

7.3.2.3 Older forests (> 50 years)

In the data examined for this thesis species richness of mature forest taxa was highest in old growth forests. Doran et al. (2003) observe that total species richness reaches a peak at some sites at about 70 years. Species richness was highest when the cover of pioneer and rainforest species was approximately even.

The longitudinal study by Ashton (2000) showed that among the species which were present in *Eucalyptus regnans* forests which at the end of the study were nearing 100 years since wildfire, only the ground fern *Blechnum nudum*, the grass *Tetrarrhena juncea*, and the herb *Hydrocotyle hirta* had not been previously recorded in the ground layer in the earlier stages of forest development.

Ashton (2000) observed that the species that increased the most between 25 to 50 and 75 to 100 years since wildfire in a Victorian *Eucalyptus regnans* forest was the shade-tolerant plant *Olearia argophylla*, which established new stems by layering and also germinated beneath senescing patches of short-lived species such as *Cassinia aculeata* and *Olearia lirata*. Although Ashton (2000) observed seedlings of the wind-dispersed rainforest tree species, *Atherosperma moschatum*, they failed to establish except in mature eucalypt forest patches immediately adjacent to riparian rainforest. *A. moschatum* was only located in one plot in the Serong (2007) data set. However, there are several shade-tolerant rainforest species (including *Nothofagus cunninghamii, Bedfordia arborescens, Hedycarya angustifolia)* found in mature forest plots that are rarer in younger forest plots (Serong 2007). Serong (2007) also shows that *Tetrarrhena juncea* and the tree ferns (*Dicksonia* and *Cyathea* species) are considerably more abundant in old growth *E. regnans* forest compared with

silvicultural regrowth, but these species are also frequent in the young forests. Serong and Lill (2008) demonstrate that it is the increased frequency and abundance of the early pioneer species in young communities, more than the increased frequency and abundance of most mature forest species in older communities, that characterised the floristic differences between *E. regnans* forest age-classes in Victoria. The only species missing from the silvicultural regrowth sites and present in more than two mature forest sites was the rainforest tree *Nothofagus cunninghamii*, although even it was only located at five of the 30 sites studied that had not been burnt for more than 60 years.

Based on the data reported by Ashton (2000) and Serong and Lil (2008), the prevalence of the two rainforest trees *Nothofagus cunninghamii* and *Atherosperma moschatum* appear to be substantially different between the Victoria and Tasmanian wet eucalypt forests. Lindenmayer et al. (2000) reported that *N. cunninghamii* was largely restricted to old growth forest in areas of high rainfall in the warmest quarter and in gullies. They predicted very low probabilities of occurrence for this species in areas with rainfall below 250 mm in the warmest quarter, and on mid-slopes or ridges, although where it was in the understorey with *E. regnans* it was found to be more prevalent on slopes. Apart from the interaction effect between slope and eucalypt dominance, the pattern observed by Lindenmayer et al. (2000) is similar to that observed in the present study for several individual mature forest species, and the total cover and richness of mature forest indicator species. In the present study area there was also an effect from topography, with steeper slopes and areas more exposed to the north and northwest being less likely to provide habitat for mature forest indicator species.

No modelling has occurred for rainforest tree *Atherosperma moschatum*, although its geographic range is known to have contracted since European colonisation, when it became locally extinct in the Otway Ranges (Lunt 1992). A sediment core from this region has demonstrated that rainforest was somewhat more widespread 7000 years BP when the area was likely to have been cooler and wetter. It also showed that between 5200 and 4600 years BP the rainforest species were replaced in importance by wet eucalypt forest taxa (McKenzie and Kershaw 1997). Fire since that time led to an increasingly scleromorphic heathland vegetation at the core site, while *Nothofagus*

cunninghamii continued to contract to its current remnant distribution within gullies (McKenzie and Kershaw 1997).

In Tasmania, *Atherosperma moschatum* is still widespread. In eastern Tasmania it can be more common within relictual rainforest sites than *Nothofagus cunninghamii* (Neyland 1991). In contrast, there are a suite of rainforest species that are completely absent from the northeast of Tasmania. Their absence is not due to the elimination of rainforest from this region during the glacial since there is evidence that refugial habitat was retained in the area, which enabled the persistence of *Eucalyptus regnans, Nothofagus cunninghamii* and *Tasmannia lanceolata,* despite increased aridity (Byrne et al. 2011). Species not found in northeastern Tasmania are *Eucryphia lucida, Anodopetalum biglandulosum, Cenarrhenes nitida, Prionotes cerinthoides,* all taxa most common within areas with high rainfall and acidic soils in western and southern Tasmania.

Seedlings and saplings of the common mature forest trees were infrequently recorded in the plots and were no more frequent in mature forest plots (Figure 7-D). In combination these data suggest that most species that have the potential to form the mature forest community are likely to have colonised regrowth patches within the first 50 years. However, the abundance of most common mature forest species remains low during the early phase in the development of these forests (Figure 7-D).

7.3.3 Overview of successional trajectories

The narrow environmental niche occupied by *Eucalyptus regnans* is reflected in the reduced variability of floristic associations it forms (Kirkpatrick et al. 1988). Regrowth aged *E. regnans* is typically associated with understoreys in which *Pomaderris apetala* is important together with species such as *Acacia dealbata, Olearia argophylla* and *Dicksonia antarctica* (Kirkpatrick et al. 1988; Ashton 2000; Serong and Lill 2008). Such understoreys are commonly also dominated or co-dominated by *E. obliqua* at drier or more frequently disturbed sites (Ashton 1981b). Floristic affinities and a shared environmental niche suggest that the successional trajectory of forest understoreys dominated by *P. apetala* is to rainforest understoreys with affinities to callidendrous rainforest (*sensu* Jarman et al. 1984). However, in

warmer drier environments less suited to the development of rainforest (*sensu* Jarman and Brown 1983), it is likely that *Olearia argophylla* and tree ferns will form an alternative successional end point for old growth forest such as are described for Victorian *E. regnans* forest. Both *O. argophylla* and *P. apetala* are important dominants of the dry rainforests described for eastern Tasmania (Pollard 2006). However, within the present study mature forests were rarely observed without rainforest species being present, and given their greater height potential than *Olearia* and *Pomaderris*, it seems probable that they will eventually achieve dominance where this is not already the case.

On acidic soils, the understoreys of young regrowth forest are usually dominated by narrow leafed and prickly plants such as *Nematolepis squamea, Acacia verticillata, Monotoca glauca* and the tussock sedge *Gahnia grandis. Eucalyptus regnans* is never present in sites with extremely poorly drained and acidic soils, but in areas of intermediate fertility and drainage associations which include both *Nematolepis squamea* and *Pomaderris apetala* either or both *E. obliqua* and *E. regnans* may be dominant. The descriptions of wet forest communities by Kirkpatrick et al. (1988) and re-examination of the state-wide data sets provide evidence that the successional end point for these communities is to mixed forest communities with affinities to thamnic rainforest (*sensu* Jarman et al. 1984) and are usually dominated by *E. obliqua*. In situations where rainfall and temperature exclude rainforest species, the vegetation associated with poor soils is more likely to be classified as dry *E. obliqua f*orest, a vegetation type not considered as part of this thesis.

7.4 Landscape context effects within pioneer species groups

There was a significant decline in the richness of pioneer ferns with distance away from mature forest in the young silvicultural regrowth. This result was due to the spatial distribution in two hygrophilous plants, *Histiopteris incisa* and *Hypolepis rugosula,* for which the most likely source populations were the adjacent mature forest. Both these ferns are pioneer rainforest species, which were included among the pioneers because of their greater importance within very young regrowth communities compared with mature forest. In contrast, the cover of the other pioneer fern, *Pteridium esculentum,* increased with distance from the boundary, supporting the theory that mature forest was not an important propagule source for this species, which mostly recovers vegetatively from rhizomes. The trend in these fern species although suggesting micro-climatic variation across the distance gradient, was more likely to have been due to propagule arrival rates. Baker et al. (2014) found that the depth of climatic influence did not extend far enough beyond the mature forest edge in these young sites for microclimate to be contributing to the observed trend.

The species groups which appeared to be most responsible for the increase in pioneer richness with increasing isolation from mature forest included those dispersed by vertebrates and those germinating from the soil-stored seed bank. This is consistent with mature forest being either unimportant as a seed source or there being some obstacle to establishment by these species close to the boundary of mature forest, during the first ten years.

Browsing pressure by marsupials is a major barrier to plant establishment in regenerating eucalypt forest (Cremer 1969; Dickinson and Kirkpatrick 1986). Total biomass and species richness is higher in fenced areas compared with unfenced areas of young forests (personal observations, Dickinson and Kirkpatrick 1986). Some studies have demonstrated a decline in browsing activity with increased distance away from forest margins (e.g. Wahungu et al. 1999). In a study of Tasmanian timber plantations, a decline in browsing damage with distance from habitat edge was observed in one third of plantations studied (Bulinski and McArthur 2000). Varying palatability is likely to contribute to variation in survival rates among species. At least one study in tropical forest has demonstrated that fast-growing pioneer species are

characterised by few defences against browsing (Coley 1983). However, Dickinson and Kirkpatrick (1986) reported that excluding browsers in regenerating dry eucalypt forests increased the growth of woody plants and graminoids at the expense of forbs and grasses. Browsing has been reported as a barrier to the recruitment of several slow growing rainforest canopy trees in Tasmania, including *Atherosperma moschatum* and *Athrotaxis cupressoides* (Cullen and Kirkpatrick 1988; Neyland 1991). Hence, it is not useful to generalise browsing responses in pioneers or mature forest species groups as a whole.

As previously noted, variation in colonisation of recently disturbed forest is known to be very closely associated with fire intensity and mechanical disturbance (Gilbert and Cunningham 1972; Cremer et al. 1978; Hindrum et al. 2012; Baker et al. 2013a). Harvested areas adjacent to stream side reserves are likely to be associated with lower fire intensity, compared with both upslope positions and adjacent ridges away from streams. Hence, it is likely that some portion of the observed decline in total richness and the increase in pioneer richness has been caused by uneven distributions in fire intensity and mechanical disturbance, rather than from mechanisms described by Baker et al. (2013b) as mature forest influences, such as root competition, litter deposition, shading, differential browsing pressure, or competition from mature forest species. At many harvested sites, it is not uncommon for the remnant patches of mature forest to be confined to the streamside reserves established to protect water quality.

Bradysporous plants also showed a somewhat weak increase in richness from the mature forest boundary. This result suggests that there were local seed sources in adjacent forest on the opposite sides of the coupe, and absent in mature forest. The seed is usually released after the plants are killed or damaged by fire, so for these species, the effect of the regeneration burn punching into the adjacent forest margin, even by just one metre, could lead to the increased release of seed, although it is likely that some capsules release seed at other times, particularly in response to plant death or drought (Specht et al. 1958). The influence of vegetation in other areas surrounding the coupe on the regenerating forests within the coupe was not investigated for the data set in chapter 3. However, Hill and Read (1984) and Brown et al. (2002) described situations where *Leptospermum* species were able to colonise new areas

beyond their previous range after fire. The abundant fine seeds of this taxa are dispersed well in strong wind (Hill and Read 1984). *Leptospermum* species were common within the regrowth of old fields, also demonstrating their capacity to invade sites with a long history of disturbance. The fact that bradysporous plants and those with soil stored seed are associated with areas of higher fire intensities (Hindrum et al. 2013) may also have contributed to the spatial patterns of richness observed here, if fire intensity also co-varies with distance from the mature forest edge, which seems quite likely at many sites.

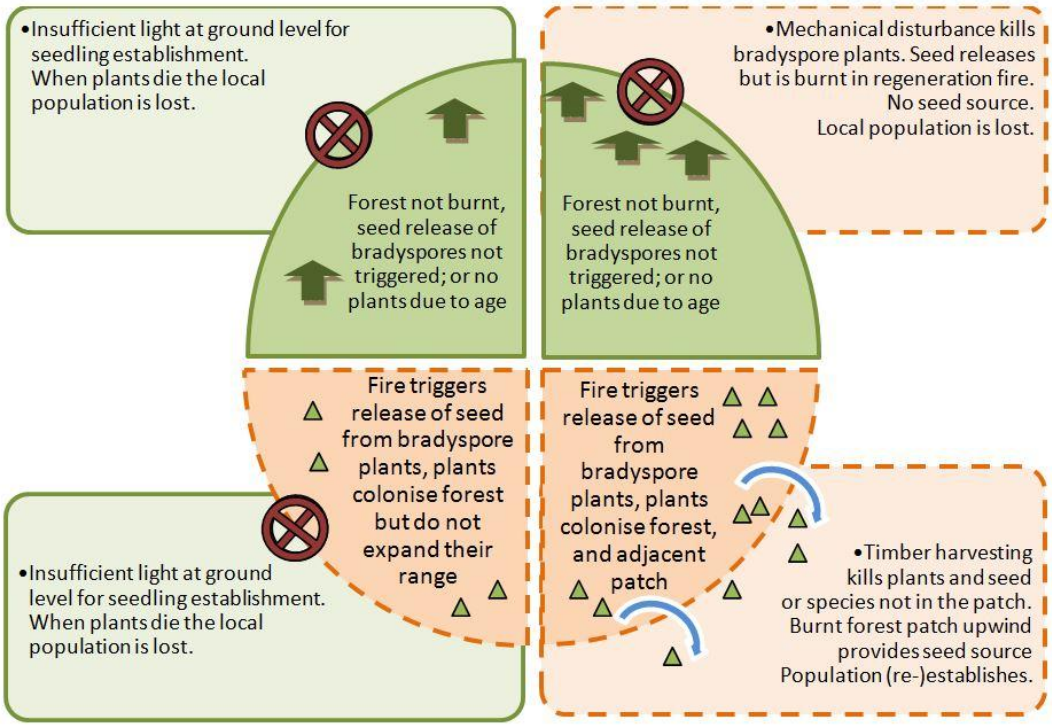


Figure 7-E. Potential changes in population for bradysporous plant species as a consequence of disturbance by wildfire (circle), timber harvesting (rectangles) or remaining undisturbed for periods of time longer than the life of the plant species.

It is unlikely that common species with soil-stored seed banks will be vulnerable to rapid population reductions due to timber harvesting. Nevertheless species with only small seed banks could be at risk if mechanical disturbance triggers germination that is then killed by fire, or the fire is so intense that the seeds are killed.

Wind-dispersed taxa are likely to be able to regenerate providing there is a windward source of live plants of reproductive age is available to supply seed in the first decade of disturbance (Figure 7-E).

The bird-dispersed taxa are likely to benefit to the greatest extent by repeated disturbance, timber harvesting and, as was demonstrated by the study of old fields, the abandonment of cleared land areas. However, recolonisation of these species is known to be improved if live or dead trees and logs are retained within the harvest area, to serve as perches to encourage stop-overs by birds (Toh et al. 1999; Elgar et al. 2014). Other research has also demonstrated that the size of fruit is a limitation to species dispersal making the populations of *Cenarrhenes nitida* more vulnerable to impacts from reductions in mature forest habitat sources, particularly since this species was less frequently observed in regrowth forest.

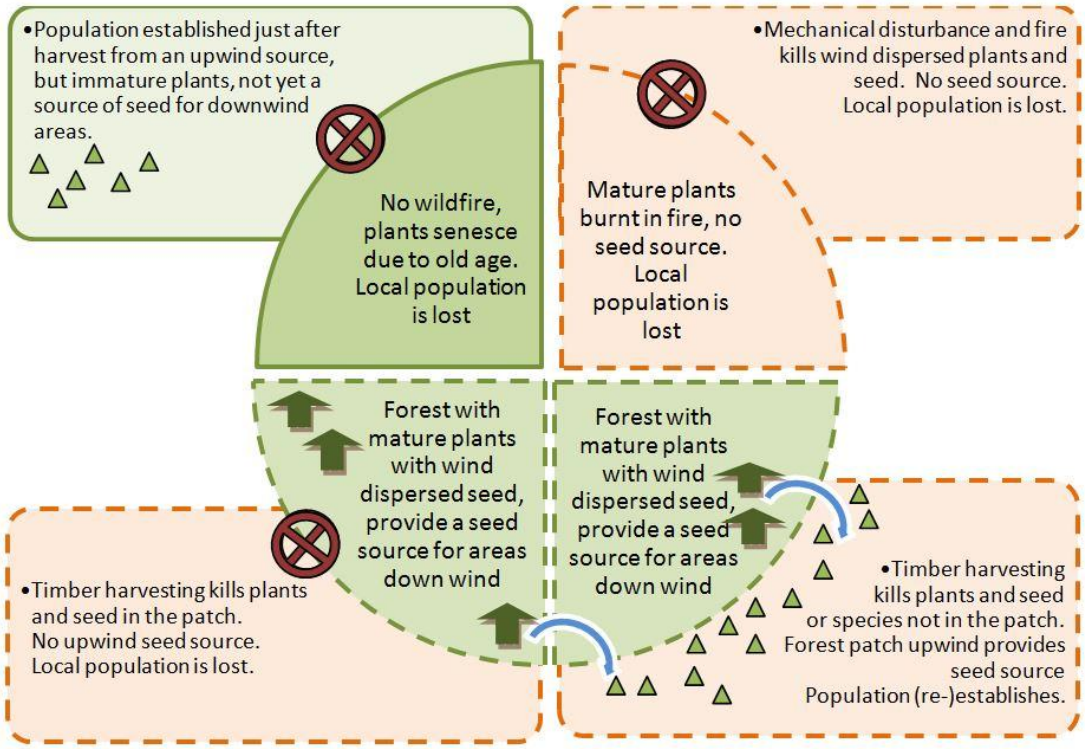


Figure 7-F. Diagrammatic illustration of potential changes in population for wind dispersed plant species as a consequence of disturbance by wildfire (circle), timber harvesting (rectangles) or remaining undisturbed for periods of time longer than the life of the plant species.

7.5 Proposed narrative for landscape context influence through time

In section 7.3 it was established that the main opportunity for colonisation by woody species is substantially limited to the period between disturbance and canopy closure, when growth rates are most rapid due to high light and nutrient availability. However, LC, if defined as the vegetation of the surrounding matrix, has only a limited capacity to directly influence the early colonisation at the site by pioneers, since many of these species re-establish from biological legacies from the pre-disturbance forest and others are able to arrive from relatively distant propagule sources. If LC is defined more broadly to include the vegetation at the site prior to disturbance then the capacity of LC to influence pioneer species colonisation is clearly much greater.

LC, as originally defined, is more strongly influential in the establishment of mature forest species following timber harvesting compared with either pioneer species or following wildfires, due to the reduced importance of biological legacies. Although these mature forest species have a greater capacity to colonise forest beyond canopy closure, sites colonised early after disturbance by mature forest species develop more rapidly to a mixed forest assemblage. The pioneer species are indirectly influenced by LC due to their competitive disadvantage in areas where mature forest species are able to colonise. Hence, many pioneer species were negatively associated with mature forest metrics, although notably not the sub-canopy dominant of fertile sites, *Pomaderris apetala,* or the ground cover of poor soils, *Gahnia grandis*.

LC will provide little influence where mature forest species are unable to colonise. These include old fields and areas where climate and topography combine to create a barrier to colonisation, such as steep, north to northwesterly aspects, in warm and dry areas. Where soils are fertile *Pomaderris apetala* is a common dominant of such sites, and on old fields, a variety of pioneers from the local area are common.

Ongoing colonisation by mature forest species, particularly of epiphytic ferns and ground cover species, will continue after canopy closure where mature forest influence is able to operate. However, the presence of many long-lived plants, including many that expand and regenerate vegetatively in the absence of fire, means

that turn-over in species happens only slowly, and the effects of the landscape configuration at the time of regeneration is likely be reflected in stand assemblage until the next fire. Losses of mature forest in surrounding landscapes after canopy closure are likely to lead to the slowing of species richness accumulation within patches, and reduce the opportunity for uncommon late-stage rainforest species to reach the patch. Nevertheless, the early colonists of mature forest species will eventually become a source of propagules when they reach sexual maturity, enabling an increase in populations of mature forest species within the patch over time.

Table 7-C. Table describing rate of community succession from four different starting points

Pre-disturbance Vegetation (previous fire intervals)	**Landscape Context Index**	**Post disturbance**	**Notes**
Mixed forest (long)	> 6	Pioneer richness low; Rich in rainforest pioneers; Population recovery by mature forest species good; **Fast return time to mixed forest.**	High rate of resprouting (e.g. *Anodopetalum*, *Atherosperma*, *Dicksonia*, *Eucryphia Nothofagus*, etc) Pioneers that persist at lower levels in mixed forest may be more important post-disturbance, particularly those with soil seed bank and seed dispersed by vertebrates (e.g. *Coprosma, Cyathodes, Gahnia, Histiopteris, Hypolepis, Leptecophylla, Monotoca, Pimelea, Pteridium*) Rapid re-establishment by rainforest species with soil seed bank (e.g. *Acacia, Phyllocladus*) bird dispersed seed (e.g. *Aristotelia, Cenarrhenes. Gaultheria, Phyllocladus, Tasmannia, Trochocarpa* etc) or wind dispersed seed (e.g. *Anopterus, Lomatia, Olearia, Orites*)
Mixed forest (intermediate)	4-6	Mixture of pioneer species and resprouting rainforest plants dominant; Pioneer richness medium; MFI species richness medium where adjacent to mature forest; **Medium return time to mixed forest**.	High rate of resprouting rainforest species Pioneer species arise from soil seed banks (*Acacia*, *Correa*, *Monotoca*, *Nematolepis*, *Pomaderris, Prostanthera*, *Zieria*) A few mature forest species and more pioneer species with wind (including bradyspores) and bird dispersed seed, colonise from surrounding area
Wet Forest (intermediate)	4-6	Pioneer species dominant; Pioneer richness low to medium; MFI species richness low in areas adjacent to mature forest, but otherwise absent; **Long return time to mixed forest.**	Mature forest species do not recover by coppicing, but rely on seed dispersed from adjacent mature forest patches (*Atherosperma*, *Nothofagus cunninghamii*, *Olearia argophylla*). Mature forest species dispersed by wind and vertebrates present only near the mature forest edge. Pioneers out-compete mature forest species elsewhere.
Forest <50 years & Old fields (short)	< 4	Pioneer species dominant; Pioneer richness high; Mature forest species negligible; Vertebrate dispersed species, higher. **Alternative trajectory.**	Rapid recovery and dominance of all pioneer species from legacy plants and seed from pre-disturbance community, and from wind and bird-dispersed seed from surrounding landscape. Only rainforest species are pioneer plants with long distance dispersal capacity (e.g. *Coprosma*).

7.6 Feedbacks reinforcing mixed forest and wet sclerophyll forest as alternative stables states

Table 7-D. A list of twelve correlated environmental factors which tend to exclude or favour the development of species of wet sclerophyll or mixed forest.

Factor levels favouring wet sclerophyll forest	Factor	Factor levels favouring mixed forest
Large (> 30 ha)	**Disturbance size**	**Small** (< 5 ha)
Short (< 50 years)	**Time since last disturbance**	**Long** (> 110 years ago)
Short (< 80 years) Note if short disturbance intervals are repeatedly short, e.g. two less than < 30 years apart, there will be a risk of converting wet forest to dry forest savannah or scrub, especially on lower fertility substrates or shallow soils.	**Previous disturbance interval**	**Long** (> 150 years)
High (most plants killed, mineral soil exposed, ash-bed created) Note that while pioneer species are favoured by high intensity disturbance compared with mature forest species, there are a range of responses among pioneer species, more of which are favoured by less intense disturbance.	**Disturbance intensity**	**Low** (some plants survive and resprout, litter remains and aids soil moisture retention, log and branch-wood remain and protect seedlings from browsing)
Medium to Long Note that while pioneer species usually re-establish populations more quickly after medium to long disturbance intervals compared with mature forest species, there are a range of responses among these species, most of which are favoured by shorter disturbance resonance times.	**Disturbance resonance time**	**Short** (humus doesn't burn and smoulder over a long interval; mechanical disturbance not following months later by intense regeneration burn; Site not cleared mechanically, burnt and continuously grazed)

Factor levels favouring wet sclerophyll forest	Factor	Factor levels favouring mixed forest
Warm /Dry (> 10.0 mean annual daily temperatures, mean max temperature in the warmest week of > 20.0 C < 1500 mm annual rainfall, < 250 mm warmest quarter, < 80 mm mean rainfall in driest month)	**Climate**	**Cool/Wet** (< 10.0 mean annual temperatures, mean max temperature in the warmest week of < 20.0 C < 1500 mm annual rainfall, < 250 mm warmest quarter, < 80 mm mean rainfall in driest month)
Exposed Northwest & northerly aspects Steep north-northwesterly slopes >20%, upper slopes, ridge and hill crests, and convex topography	**Topography** (i.e. exposure to sunshine, wind, fires)	**Protected** South to southeasterly aspects Gullies, Lower slopes < 20%, Riparian flats, basins, sinks, and other concave topography, ledges at break of slope
Small (< 10%)	**Area of mature forest** (in 1km radius)	**Large** (> 50%)
Far (> 150 m)	**Proximity to mature forest**	**Close** (< 50 m)
Simple (absence of litter, branch-wood, logs or standing dead or alive trees) Note that while pioneer species usually re-establish populations more quickly in areas devoid of structure following disturbance compared with mature forest species, there are a range of responses among these species, many of which are favoured by more complex structures.	**Forest structure following disturbance**	**Complex** (presence of litter, branch-wood, logs and standing dead and alive trees)
Low (?) Pioneer species as a group are not favoured by browsing but some less palatable individuals may benefit from the reduced competition from more palatable species when intense browsing occurs.	**Browsing pressure**	**Medium** (?) Mature forest species as a group are not favoured by browsing but some less palatable individuals, e.g. *Nothofagus cunninghamii* and *Tasmannia lanceolata* benefit from the reduced competition from more palatable pioneer species when there is moderate browsing.

Factor levels favouring wet sclerophyll forest	Factor	Factor levels favouring mixed forest
High fertility, low available moisture, well drained High growth rates and abundance of pioneer species, especially the dominant eucalypts, is greatly enhanced when available nutrients are high following fire. Shallow or clay rich soils in drought prone sites favour some drought resistant pioneer species. However, the response of individual pioneer species to soil nutrient and soil moisture varies greatly.	**Edaphic factors**	**Low fertility, high available moisture, poorly drained** The slow growth rates of mature forest species result in their having greater capacity to compete with pioneer species at lower nutrient and more poorly drained sites. Low nutrient availability and high soil moisture availability favour a greater importance of Tasmanian endemic rainforest species such as *Eucryphia lucida* and *Anodopetalum biglandulosum.*

7.7 Tenure and reservation status of mature forest

Table 7-E. Mature forests and old growth forests reserved in the study area

Tenure	Reserved areas	Old growth & mixed forest and rainforest	Mature forest disturbed in last century	All Mature forest including rainforest
National Park	11,720	5766	2360	8,126
Regional Reserve	4622	1600	749	2,349
Conservation Area	5332	1396	1313	2,709
Private reserve perpetual	56	0	0	0
Other private reserve (variable rotation)	82	0	1	1
Informal reserve on State Forest or Forestry Tasmania managed land (Tasmanian Forest Agreement- first proposed reserve order)	1602	578	378	955
Informal reserve forest on State Forest or Forestry Tasmania managed land	4919	1355	506	1,861
Other informal reserve	6	0	0	0
Not included in the CAR reserve system (unreserved)	46738	2236	2722	4,958
% of area not reserved	64%	17.3%	34%	24%
State forest in coupes		1293	1609	2902
State forest in informal management zones		585	713	1298
Total (ha)	72600	12931	8028	20,959
Proportion of study area	100%	18%		29%

Chapter 8 Part B References

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